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APEX

Effect of temperature on noradrenaline and adrenaline content in the brain of a terrestrial slug, *Laevicaulis alte* (Férussac) (Gastropoda : Soleolifera)

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KEYWORDS: Slug, brain, noradrenaline, adrenaline, temperature.

ABSTRACT: The garden slugs *Laevicaulis alte* (Férussac) were exposed to 10°, 15°, 20°, 25°, 30° and 35°C constant temperatures to study the changes in noradrenaline and adrenaline contents in the brain. Depletions in the amount of noradrenaline at 10° and 20°C, and elevations in the amount of both noradrenaline and adrenaline have been noted at 15° and 30°C. Both noradrenaline and adrenaline contents at 25°C were found almost equal. No change in adrenaline content was noted at 10° and 20°C while the amount was appreciably high at 35°C.

INTRODUCTION

The garden slugs *Laevicaulis alte* (Férussac) have a wide range of temperature tolerance (GODAN, 1983; RAUT and MANDAL, 1984). They are found active in monsoon at a temperature range 14° - 35°C. In winter when the temperature falls below 12°C, they hibernate to overcome the temperature-induced environmental hazards. Though the behavioural changes are well marked, the factors influencing such changes are still not known, although the neuroendocrine system of the animal is generally presumed to be involved. The present experiments therefore examined variations in amount of noradrenaline and adrenaline in the brain of *L. alte* (Férussac) under different fixed temperatures.

MATERIALS AND METHODS.

Gravid *Laevicaulis alte* (Férussac) were collected from their natural habitat at Sandeshkhali, 24-Parganas (North), West Bengal, India. They were reared under laboratory conditions (at room temperatures 21.6° - 30.4°C) following the method described by RAUT (1991) to obtain the slug individuals as per requirement of the study. A total of 90 laboratory-reared, adult, healthy individuals with 57-60 mm in body length, 19-21 mm in body breadth and 3.27-3.62 g in body weight were divided into 6 groups. Each group was housed separately in a terrarium measuring 30 x 20 x 15 cm, provided with loose, moist soil up to 6 cm of its height. Each of the 6 terraria was exposed to any of the constant 10°, 15°, 20°, 25°, 30° and 35°C temperature grades maintained in 6 separate Biological Oxygen Demand (B.O.D.) incubators (S.N. Mullick, Calcutta). (The atmospheric temperature of Sandeshkhali area ranges from 10° - 35°C). The moisture of the soil was kept between 37 - 40 % in all terraria throughout the experiment by spraying water at a regular interval. A favourable humidity range (80 - 90 %) was also maintained inside the chambers throughout in the same way. Also the slugs were exposed to light (400 Lux) provided by a 15 W. bulb for a period of 12 hours. The slugs were supplied with lettuce (*Lactuca sativa* Linnaeus) and beans (*Lablab purpureus* Linnaeus) regularly in excess as their food. Strict hygienic condition was maintained throughout by removing the unconsumed food matters and the faecal pellets. The experiment was continued for a period on one month.

For the collection of brain (including all associated ganglionic parts), in each case, the slugs (5 individuals) were anaesthetized by applying chloroform prior to dissection. The materials were then processed for the spectrophotofluorometric determinations of noradrenaline and adrenaline following COX and PERHACH (1973) and LAVERTY and TAYLOR (1968). The estimation of the monoamines present in the samples was made by the help of a Hitachi (Model 650-10 M) Fluorescence Spectrophotometer (for details see MAHATA and GROSH, 1989). The experiments were repeated thrice and the mean of three readings of pooled observations was considered as the actual amount of noradrenaline and adrenaline present

in the brain. Statistical analysis of the data was performed following GOON et al. (1976).

RESULTS

The slugs survived for a period of 9-15 days at 10°C, 24-29 days at 15°C and 6-9 days at 35°C temperatures. In the remaining groups, none died during the period of 30 days.

The autopsy for the collection of brain was done on the 9th, 24th and 6th day of exposure of slugs maintained at 10°, 15°and 35°C, respectively, as the death was started on these days. In these cases, five individuals were considered for autopsy. The remaining individuals (except those died on that day) were maintained as usual, at these temperatures till the death of all individuals. The average weight of the brain was 4.05 mg. Noradrenaline and adrenaline content recorded from the brain of *L. alte* (Férussac) maintained under different temperature grades have been shown in Table 1. To justify the validity of the data obtained in respect to different temperatures, the two-way fixed effect homoscedastic Analysis of Variance (ANOVA) was applied (Table 2). From the results, it is clear that there exists a significant difference at 1 % level among noradrenaline and adrenaline in *L. alte* in respect to different temperatures. Also, the degree of interaction between monoamine and temperature is significant throughout.

To study the maximum significant effect of monoamine (noradrenaline or adrenaline), temperature and interaction due to monoamine and temperature, we adopt Student's 't' test through pair comparison. In general, for (**ij**)th pair, if absolute difference of means of (**ij**)th pair is greater than

$$t_{\alpha/2,\mathrm{df}}\sqrt{\mathrm{MSE}}\sqrt{\frac{1}{n_i}+\frac{1}{n_j}}$$

(called least significance difference (l.s.d.), then, (**ij**)th pair is significant at α% level of significance. In our case, l.s.d. for effect of monoamine is

$$t_{\alpha/2,\mathrm{df}}\sqrt{\mathrm{MSE}}\sqrt{2/3}=2.49\sqrt{0.1533}\sqrt{2/18}=0.3250$$

at 1% level of significance.

Similarly, l.s.d. for temperature is

$$2.49\sqrt{0.1533}\sqrt{2/6}=0.5629$$

and l.s.d. for interaction between effect of monoamine and temperature is

$$2.49\sqrt{0.1533}\sqrt{2/3}=0.7960$$

It is evident that adrenaline and 35°C have maximum significant effect (Table 1).

DISCUSSION

Ample evidences demonstrate the presence of monoamines in the central nervous system for vertebrates (TURNER and BAGNARA, 1976; LANDSBERG and YOUNG, 1985). In molluscs, catecholamine containing cell bodies have beeen demonstrated in *Limax maximus* Linnaeus (OSBORNE and COTTRELL, 1971), *Aplysia* (GOLDSTEIN, 1984), *Helisoma* (TRIMBLE et al., 1984), *Helicella virgata* DaCosta (FRANCHINI et al., 1985) and *Lymnaea stagnalis* Linnaeus (AUDESIRK, 1985). The distribution of monoamines in the central nervous system of gastropods, *Hermissenda crassicornis* Eschscholtz and *Achatina fulica* Bowdich has been described by CROLL (1987a, b, 1988). VON EULER (1953) reported the presence of noradrenaline in *Octopus*. McCAMAN et al. (1979a, b, 1984) were successful in isolating dopamine, 5-hydroxytryptamine and N-acetyldopamine from molluscan ganglia. GERSCHENFELD (1973) and LEAKE and WALKER (1980) are in opinion that dopamine is the major catecholamine of the snail *Helix*. Though OSBORNE and COTTRELL (1970) and JUORIO and KILLICK (1972) noted the presence of significant amount of noradrenaline in the brain of *Helix* and some other molluscs quantitative data of the amount of noradrenaline and adrenaline in molluscs, in the true sense, was not available until the publication of OSBORNE's (1984) work on CNS of *Helix aspersa* Müller.

Subsequently, COON and BONAR (1986) were also successful in quantifying the amount of norepinephrine and dopamine in the larval and spat stages of the Pacific Oyster *Crassostrea gigas* (Thunberg). Recently, findings by PANIGRAHI et al. (1992) not only demonstrate the amount of noradrenaline and adrenaline in the brain of the slugs *L. alte* (Férussac) but also provide information on fluctuations in the amount of these monoamines at different hours of a day. However, none of the previous workers has paid attention to study the effect of temperature on monoamine content in the brain of any mollusc. On the contrary, such a study is on record in some vertebrates - reptiles (REITER, 1981); birds (HARVEY et al., 1984) and mammals (TURNER and BAGNARA, 1976; LANDSBERG and YOUNG, 1985). The present findings clearly indicate that temperature has great influence on noradrenaline and adrenaline content in the brain of the slugs *L. alte*. Variations in the amount of noradrenaline and adrenaline recorded in the brains of *L. alte* in respect to temperatures seem to be related with the functional status of the enzymes involved with the process of synthesis of these amines. This

phenomenon has been discussed by OSBORNE (1984) in case of the gastropod snail *H. aspersa*. Whatever be the reasons for such changes in amine contents, it seems that the phenomenon is involved with the steps of adjustment of the concerned slugs in respect to the conditions evolved due to change of temperatures. Though further experimental studies are needed to evaluate the role of temperature in influencing the rate of release of monoamines it is sure that the said factor constitutes a potential source of interference.

Acknowledgments

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Table 1.
Noradrenaline and adrenaline content (average ± S.E.) in the brain of the garden slugs *Laevicaulis alte* maintained under different temperature grades for a different length of time (not more than 30 days in any case) depending upon their withstanding capacity under such conditions [Remarks refer to the concentrations of noradrenaline and adrenaline at the same temperature].

Temperature (°C)	Monoamine (μg/g tissue ± S.E)		t-value		Remarks
	Noradrenaline	Adrenaline			
10*	6.77 ± 0.21	9.62 ± 0.24	10.514	(p = 0.01)	S
15**	14.58 ±0.29	11.34 ± 0.25	8.510	(p = 0.01)	S
20	2.32 ± 0.11	9.45 ± 0.32	21.221	(p = 0.01)	S
25	9.27 ± 0.18	9.41 ± 0.11	0.623		NS
30	10.16 ± 0.26	10.28 ± 0.22	0.208		NS
35***	10.12 ± 0.25	19.31 ± 0.07	35.868	(p = 0.01)	S

* The slugs survived for a period of 9-15 days.

** The slugs survived for a period of 24-29 days.

*** The slugs survived for a period of 6-9 days.

S = Significant, NS = Not significant.

Table 2.
Analysis of Variance (ANOVA) to justify the effect of monoamines (noradrenaline and adrenaline in respect to different temperature grades in the brain of the garden slug *Laevicaulis alte*.

Source of variation	df	SS	MS	F_{Cal}	F_{tab} (α = 1%)
Effect of monoamines (E)	1	64.7220	64.722	422.131	7.87
Temperature (T)	5	305.9037	61.1807	399.034	3.93
Interaction (E x T)	5	163.3672	32.6734	213.103	3.93
Error	24	3.6797	0.1533	-	-
Total	35	537.6726	-	-	-

The Orbitestellidae (Gastropoda: Heterobranchia) of the Sultanate of Oman with description of a new genus and two new species*

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ABSTRACT. Three species of the family Orbitestellidae are recognized from Oman . The first, *Orbitestella bermudezi* (Aguayo & Borro, 1946) was previously known from the tropical Atlantic Ocean. It is also recorded from the Red Sea. The two remaining species are new to science and require a new genus. *Boschitestella* nov. gen. with *B. donaldi* nov. sp., known from Oman, Red Sea, Thailand and Indonesia and *B. eloiseae* nov. sp. only known from Oman are assigned to this new genus.

KEYWORDS: Gastropoda, Orbitestellidae, *Orbitestella* , *Boschitestella* nov. gen, Indian Ocean, Oman.

INTRODUCTION

Because of their minute size, species of the family Orbitestellidae have been overlooked in most marine faunas. However, during recent years much progress has been made in the understanding of these very small gastropods. PONDER (1990) showed that the orbitestellids are primitive heterobranchs. Up to now most species were recorded from the southern hemisphere (especially [sub]Antarctica, Australia, and New Zealand) but recently some recordings have been made from the northern hemisphere. KAY (1979) described a new species from Hawaii. FABER (1991) and ROLAN & RUBIO (1992) recognized their existence in the western and mid Atlantic Ocean.

During fieldwork along the coastline of the Sultanate of Oman in November 1991, a limited number of these microgastropods were found in the intertidal zone, beneath rocks and among coralline algae. In our samples two types with different characters are distinguished. One with the typical outline of the genus *Orbitestella* Iredale, 1917 and shells of the other group are distinguished by only one single, sharp carina on the periphery of the teleoconch. These are considered here to belong to a new genus.

*Studies on the marine molluscan fauna of Oman, n°. 9.

TAXONOMY

Orbitestella bermudezi (Aguayo & Borro, 1946)
Figs 1-8

Cyclostremiscus bermudezi Aguayo & Borro, 1946: 9-12
Orbitestella similis Rolán & Rubio, 1992: 17-18
Orbitestella cubana Rolán & Rubio, 1992: 18-19

Distribution. West Indies; Cape Verde Islands; Red Sea (Gulf of Aqaba); Oman (Al Hallaniyah, Sta. 91/60, 5 specs: Masirah Island; BERS camp, Sta. 91/95, 1 spec.; Ra's al Ya, Sta, 91/105, 1 spec., all November 1991, leg. R.G. Moolenbeek & H. Dekker).

Remarks. FABER (1991) recorded *O. bermudezi* , originally described as a Cuban fossil of Miocene or Pleistocene age, being an extant species known from several West Indian islands. ROLAN & RUBIO (1992) described two new species respectively *O. similis* from the Cape Verde Islands and *O. cubana* from Cuba. If the figure numbers in ROLAN & RUBIO (1992) are correct (and not reversed) it is obvious that the figured specimen of *O. similis* is nearly identical to Faber's figured specimen from the West Indies.

After comparing specimens from several West Indian islands it is my opinion that both taxa from ROLAN & RUBIO (1992) fall within the variability of *O. bermudezi.* . Furthermore, their identical protoconchs support this view.

More remarkable is the occurrence of *O. bermudezi* in the northern Indian Ocean. Specimens from Oman (Figs 1-3) have the same type of protoconch with the minute granulations and a mid dorsal ridge (Figs 4-5). Also the sculpture of the teleoconch falls within the variation known in *O. bermudezi*. The only difference noticed is the height of the two peripheral spiral ridges. It appears slightly smaller on the figured specimen but varies in the Oman population. In a small grunge sample from the Red Sea, Gulf of Aqaba (Nuweiba), collected by Mr. C. Steenman in October 1992 this species was rather common (Figs 6-8). Again, the specimens show variability in shell morphology but are still considered to be identical to *O. bermudezi*. This exceptional large distribution pattern may be explained by its likely Tethyan origin.

TURTON (1932) described *Homalogyra gemmulata* from South Africa. This species is very similar to *Orbitestella bermudezi*, however his figures and description are too vague to give a definitive opinion. A study of the type material (Oxford University Museum, U.K.) and additional material from the Natal Museum (Pietermaritzburg, South Africa) has been initiated. Also *Cyclostrema bastowi* Gatliff, 1906, the type species of the genus *Orbitestella* might be identical and would be the oldest name for this taxon.

Boschitestella nov. gen.

Type Species: *Boschitestella donaldi* nov. sp.

Diagnosis. Shell minute, discoidal, width 0.5-0.9 mm, height 0.2-0.3 mm, widely umbilicate, translucent white , with numerous fine spiral threads, which consist of small granules (at high magnification), weak axial ribs or knobs and one spiral ridge on the periphery.

Etymology. The genus and the type species were named in honour of Dr. Donald Bosch, who stimulated my interest in the marine molluscs of Oman.

Distribution. Red Sea, Thailand and Indonesia. In Oman, from the Muscat area and from Al Hallaniyah (=Kuria Muria Islands).

Remarks. The genus is based on differences in shell morphology between species of this genus and species of the genus *Orbitestella* Iredale, 1917. The type of this genus is *Cyclostrema bastowi* Gatliff, 1906, described from Victoria, Australia. *Boschitestella* differs by its single sharp carina on the periphery, being larger and a different structure of its protoconch. Radula and soft parts are unknown.

The genus *Vitrinorbis* Pilsbry & Olsson, 1952 from the Panamic province has superficial resemblance to *Boschitestella* . However, it differs in being twice as large and having a different sculpture of fine spiral threads, cut into fine beads by close, retractively radial grooves.

Boschitestella donaldi nov. sp.
Figs 9-13

Description of the holotype (ZMA Moll. 3.93.002; width 0.86 mm, height 0.24 mm). Shell minute, translucent white, discoidal with a flat spire, widely umbilicate, strong axial plicae on the periphery and numerous fine spiral threads. Protoconch I of 0.6 whorl (diameter 0.09mm), initial part with a hexagonal, crateriform structure gradually becoming smooth and terminated by a varix. Apex slightly inrolled. Protoconch II of 0.5 whorl, smooth, terminated by a distinct varix (diameter Pc I + Pc II: 0.17 mm). Colour light tan. Teleoconch of approximately 1.8 whorls with numerous fine spiral threads on upper side and rather strong knobs on the mid part. Well developed plicae on the periphery and on the base the spiral threads diminish. Base with about 13 spiral rows gradually disappearing towards the protoconch and approximately 38 axial ribs on the body whorl.

Type Locality. Sultanate of Oman, Haramal near Muscat, Sta. 91/83, low tide, in tidal pools with rocks, 28.11.1991, leg. R.G. Moolenbeek & H. Dekker.

Variability. Two paratypes (ZMA Moll 3.93.003) from the type locality, conform favorably in all sculpture details with the holotype. Paratype 1 (fig. 11) width 0.76 mm; paratype 2, a subadult specimen (fig. 10) width 0.58 mm.

Other Material Studied. OMAN: Al Bustan near Muscat, Sta. 91/51, XI.1991, leg. R.G. Moolenbeek & H. Dekker (1 spec.). RED SEA: EGYPT, Gulf of Aqaba, Nuweiba, X.1992, leg. C. Steenman (4 specs). INDONESIA: N.E. Sumbawa, Bima Island, 10 m, IX.1987, leg. J. Veth (10 specs); Bunaken

Island, 20 m, VII.1988, leg. J. Veth (1 spec.). THAILAND: Phuket Island, Patong Beach, XII.1983, leg. J. de Visser, coll. T. Keukelaar-Van den Berge (2 specs).

Remarks. *Boschitestella donaldi* nov. sp. differs from *Orbitestella bermudezi* by having (probably) planktotrophic larval development and only one ridge on the periphery. It differs from *Boschitestella eloiseae* nov. sp. by having planktotrophic larval development, and fewer spiral threads on the bodywhorl.

Boschitestella eloiseae nov. sp.
Figs 14-16

Description of the holotype (ZMA Moll. 3.93.003; width 0.55 mm, height 0.2 mm, subadult specimen). Shell minute, translucent white, discoidal with flat spire, widely umbilicate, small axial plicae on periphery and numerous fine spiral threads. Protoconch of 1.3 whorls (diameter 0.18 mm), initial part with a hexagonal, crateriform structure gradually becoming smooth and terminated by a varix. Colour white. Teleoconch of about 1.3 whorls with many fine spiral threads on upper side (about 25) and rather strong axial ribs (about 21) . Under side with 25 fine spiral threads of which only about 5 are visible near the protoconch and about 38 axial ribs.

Type Locality. Sultanate of Oman, Al Hallaniyah (=Kuria Muria Islands) Sta. 91/60, tidal pools with rocks, 12.11.1991, leg. R.G. Moolenbeek & H. Dekker.

Variability. One paratype (0.5 mm width; 0.2 mm height) from Masirah Island, Ra's Abu Rasas, tidal pools, Sta. 91/90, 19 November 1991, leg. R.G. Moolenbeek & H. Dekker, closely resembling the holotype.

Remarks. A single species comparable to this taxon is *Boschitestella donaldi* nov. sp. However, it can be distinghuished by its different type of protoconch, indicating a non-planktotrophic larval development.

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KLM Oman (Mr J.W. Creutzberg and J. Simpson) kindly arranged a courtesy air ticket from Amsterdam to Seeb. Dr. H.E. Coomans, M.J. Faber and two unknown referees gave valuable suggestions and Mrs K. Kaiser corrected the English text. SEM photos were made at the Laboratorium voor Elektronenmikroskopie (University of Amsterdam) by the author.

APPENDIX: In the final stage of this paper, a congress lecture was published in *Venus* 51(1-2), 1992: 133-135 by S. Kaneko. He figured two unidentified orbitestellids from Japan which definitely belong to the genus *Boschitestella*. Whether these are conspecific with the Oman species needs further research.

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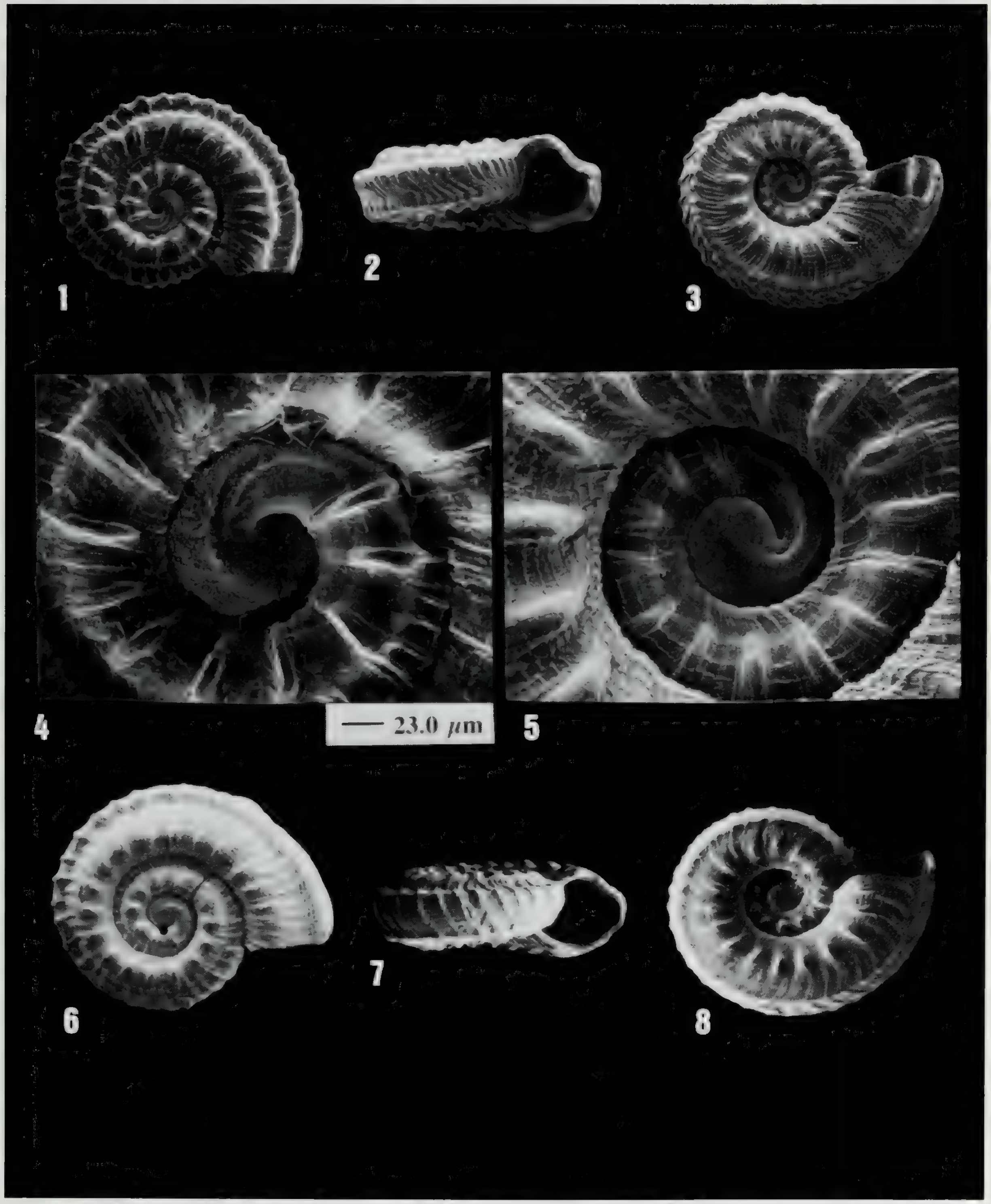
Figs 1-8. (opposite page) *Orbitestella bermudezi* (Aguayo & Borro, 1946). 1-5. Oman, Al Hallaniyah, Sta. 91/60. 1. Dorsal view, width 0.50 mm. 2. Lateral view, height 0.2 mm. 3. Ventral view, width 0.60 mm. 4-5. Detail of protoconch, dorsal and ventral view. 6-8. Red Sea, Nuweiba, X.1992. 6. Dorsal view, width 0.55 mm. 7. Lateral view, height 0.2 mm. 8. Ventral view, width 0.55 mm.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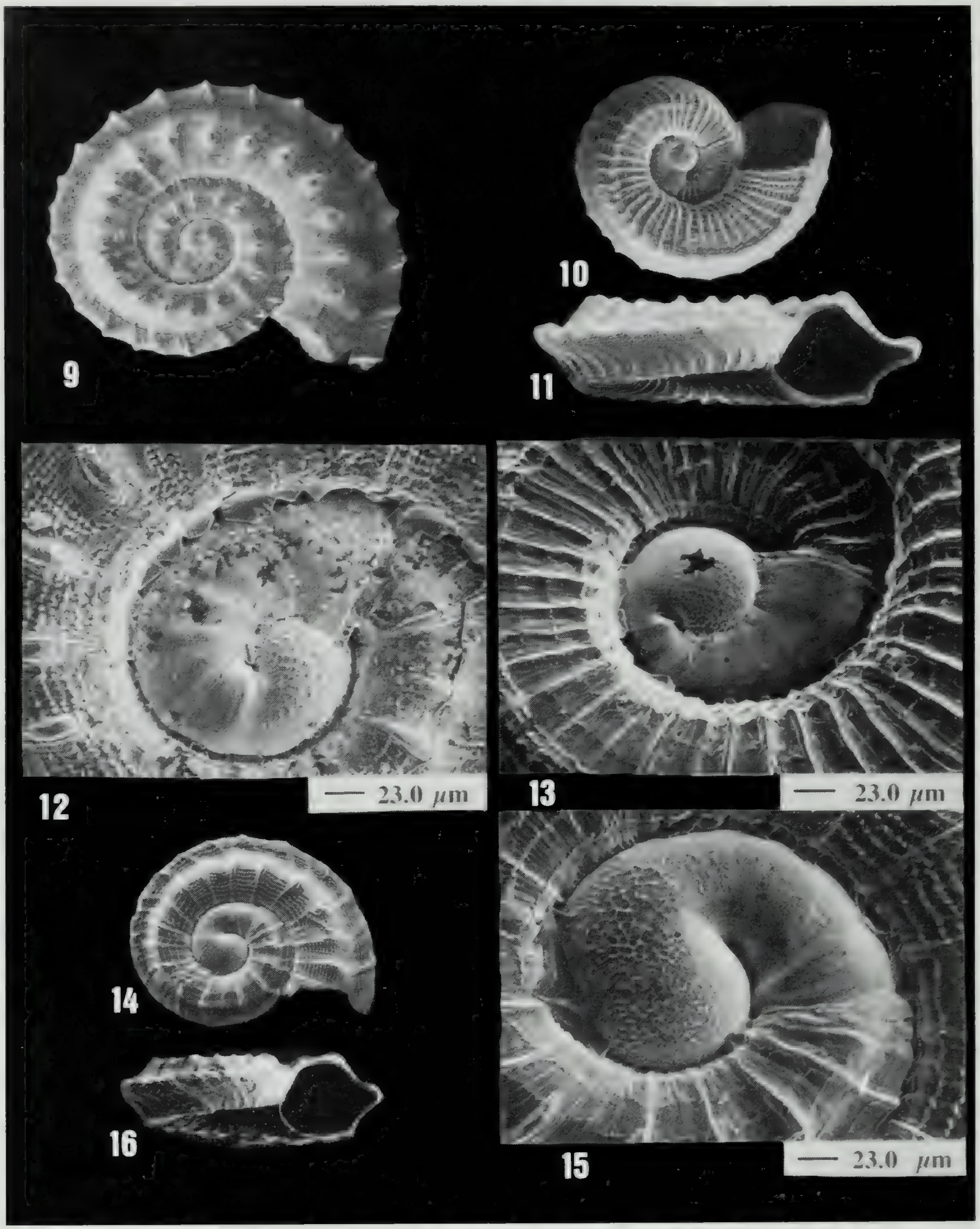

Figs 9-13. *Boschitestella donaldi* n.sp. , Oman, Haramal, Sta. 91/83. 9. Dorsal view of paratype 1, Width 0.76 mm.10. Ventral view of paratype 2, Width 0.58 mm. 11. Lateral view of holotype, height 0.26 mm. 12-13. Details of protoconch, dorsal and ventral views of paratype 1.
Figs. 14-16. *Boschitestella eloiseae* n.sp., Oman, Al Hallaniyah, Sta. 91/60, holotype. 14. Dorsal view, width 0.55 mm. 15. Details of protoconch. 16. Lateral view, height 0.20 mm.

A note on the *Museum Leskeanum*

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ABSTRACT. The *Museum Leskeanum* of D.L.G. Karsten (1789) should be considered as an available work, in the meaning of the International Code of Zoological Nomenclature.

RESUME. Le *Museum Leskeanum* de D.L.G. Karsten (1789) doit être considéré comme un travail disponible, dans le sens du Code International de Nomenclature Zoologique.

KEYWORDS: Zoological nomenclature, Karsten, available work, *Museum Leskeanum*.

The names in Karsten's *Museum Leskeanum* are generally dismissed in the malacological literature as being "non-binominal". Careful re-examination of this work shows that this opinion should be reversed.

Dietrich Ludwig Gustav KARSTEN was born in Bützow (Mecklenburg) on April 5, 1768 in a family of great scientific achievers. His father, Wenceslas J.G. KARSTEN (1732-1787) was one of the foremost German mathematicians of the 18th century, the author of many books and a professor at several universities. His uncle Franz C.L. KARSTEN (1751-1829) was a prominent agronomist, professor at Iena. His cousin Karl J.B. KARSTEN (1782-1853) was a mineralogist, author of many works, and ended as chief adviser for the mines in Berlin.

Albeit rarely cited in malacology, Dietrich Ludwig Gustav KARSTEN is very well known in mineralogy, a field of which he is considered to be one of the most important founders. He first studied mathematics and physics with his father, then enroled in 1782 in the Freyberg school of mines, where he studied for years under A.G. Werner. He was designated in 1788 to classify the mineral collection of N.G. LESKE, that was also very rich in animals. This resulted the following year in the publication of the *Museum Leskeanum*, consisting in two *in 8°* volumes. The second volume proposed a new method of classifying minerals on the basis of their natural characters and was epoch-making in the history of mineralogy. The first volume (*Regnum Animale*) is the subject of this note. After this, Karsten published numerous works on mineralogy and related fields. In 1789 he was lecturing at the University of Berlin, where he was called by the minister Heynitz. Karsten progressed rapidly in the scientific hierarchy and in 1810 he was nominated to head of the administration of sciences. He died shortly later, in Berlin on May 5, 1810.

Nathanel Gottfried LESKE, whose collection is described in the *Museum Leskeanum*, was a German naturalist born in Muskau on October 22, 1751. He was a professor at Leipzig and Marburg and published books on botany, ichtyology, physiology, etc. He died in Marburg on November 25, 1786.

The *Museum Leskeanum* (of which we will only consider the first volume, the second being devoted to minerals) consists of 320 pages and 9 plates. An exemplary is present at the Dautzenberg Library (Institut Royal des Sciences Naturelles de Belgique, Brussels). The front page is reproduced in Fig. 1.

The Volume 1 of the *Museum Leskeanum* consists of 6 parts: *Mammalia* (86 specimens), *Aves* (161 specimens), *Amphibia* (120 specimens), *Pisces* (72 specimens), *Insecta* (2576 specimens) and *Vermes* (1430 specimens). The numbering in the book concerns specimens, not species.

The voluminous part on Insects is not of the hand of Karsten, but is from one J.J. Zschach as clearly stated on the first page of the chapter (see fig.2). This interesting but separate work will not be discussed here and should be referred at as "Zschach *in* Karsten".

Availability of the *Museum Leskeanum*. To be available a work must:

a/ be published within the meaning of the International Code of Zoological Nomenclature after 1757.

b/ not be suppressed by the International Commission of Zoological Nomenclature for nomenclatural purposes.

c/ consistently apply the Principle of Binominal Nomenclature.

We shall consider these three points in succession.

a/ The book was printed in Leipzig in 1789 ("*LIPSIAE, SUMPTIBUS HAEREDUM I.G. MULLERI*"). It obviously meets the requirements of Chapter III (Criteria of Publication) of the Code.

b/ The *Museum Leskeanum* was not found in the Official Index of Rejected and Invalid Works in Zoological Nomenclature.

c/ All the descriptions of Karsten (numbering 1869) have been checked. By large, Karsten's text is consistently binominal, never referring to an animal by a vernacular name only. One entry is clearly non-binominal: "*Pinna haud ignobilis*" (p. 186, 403-404). This should present no nomenclatural problem, as it simply means: "a *Pinna* that is not of the species *ignobilis*". It is obviously not a name but, on the contrary, a disclaimer approximating our modern "*Pinna* aff. *ignobilis*". The remainder of the text still contains a number of trinomens as well as a few names that are questionable for the modern taxonomist. As examples of the most disputable cases we found, let us cite: *Arca Rhomboidalis I. Orient.* (p.173), *Cypraea Caput Serpentis* (p. 204), *Turbo Cidaris rufescens* (p. 275), *Turbo Tectum Persicum* (p. 275).

On the one hand, our first reaction was that Karsten's work is not consistently binominal and should be rejected. On the other hand, we are well aware that such departures from strict binominal nomenclature are commonplace in ancient works that are officially available in the meaning of the International Code of Zoological Nomenclature. It is obvious that the rigid requirements of the Code are *de facto* more flexible in the case of very old authors. But by how much should the rules be stretched ? We strongly feel that it is not for us to rule on this point.

In the present case, we do not even need to air our own opinions on the subject. The acceptable level of departure from strict binominality can be very simply determined by comparing (see Table 1) the major deviations to binominal nomenclature found in the *Museum Leskeanum* with some present in the *Museum Boltenianum* (Röding, 1798), a work that is approved by the International Commission of Zoological Nomenclature (Official List of Works Approved as Available for Zoological Nomenclature. Direction 48. Title 26. Publ. 21 nov. 1956). Such cases are actually very common in Röding's *Museum Boltenianum*. Amongst many others (not utilised in Table 1) let us cite: *Cassis Caput Bovis* (p. 28, n° 342), *Cassis Mitella Polonica* (p. 29, n° 357), *Conus Mille punctatus* (p. 47, n° 605), *Conus cutis anguina* (p. 619, n° 48), *Trochus Tectum chinense* (p. 81, n° 1057), *Neptunea Corona Mexicana* (p. 116, n° 1492).

Museum Leskeanum (Karsten, 1789)	***Museum Boltenianum*** (Röding, 1798)
Arca Rhomboidalis I. Orient. (p.173)	*Conus Archithalassus Indiae* (p. 43, n° 545)
Conus Cauda Erminea (p. 191)	*Bulla Ovum Vanelli* (p. 15, n° 181)
Cypraea Caput Serpentis (p. 204)	*Cypraea Caput Serpentis* (p. 23, n° 23)
Turbo Cidaris rufescens (p. 275)	*Bulla Ampulla Striata* (p. 15, n° 182)
Turbo Tectum Persicum (p. 275)	*Cidaris Tectum persicum* (p. 84, n° 1089)

Table 1. Examples of some departures from strict binominality in Karsten (1789) and in Röding (1798).

The short comparison table given here could be considerably extended, with the same result. Karsten's occasional deviations to strict binominalism are all exactly matched in Röding's *Museum Boltenianum*, published a decade later. If only for the sake of coherence, what is accepted for Röding should also be accepted for Karsten and we see no reason why the *Museum Leskeanum* names should not be available.

Comments. The work of Karsten is of incomparably higher scientific standing than the sterile, uninteresting enumeration of Röding. It is perfectly clear from the *Praefatio* that the author is conversant with the Linnean system and well aware of the distinction between generic and specific characters. He is also familiar with natural variation, as evidenced all along the text. His descriptions (see examples in fig. 3) are objective and informative. For molluscs, Karsten gives measurements of length *and* width and is thus a precursor of shell morphometry (the ratios of his measurements on *Oliva* were checked by us and found most accurate). In contrast to most of his contemporaries, Karsten gives a detailed list of references and carefully analyses his sources. Reading the *Museum Leskeanum* always gave us an impression of modernity. The author was obviously quite in advance on his time, as attested by his fame in another field, mineralogy.

ACKNOWLEDGEMENTS. We thank Dr. J. Van Goethem (I.R.Sc.N.B.) for access to the books of the Dautzenberg Library. We are specially grateful to Mr Antoine Lievrouw (I.R.Sc.N.B.) for his kind and constant help. We thank Dr. Henry Coomans (Zoölogisch Museum, Amsterdam) for his friendly and valuable advice.

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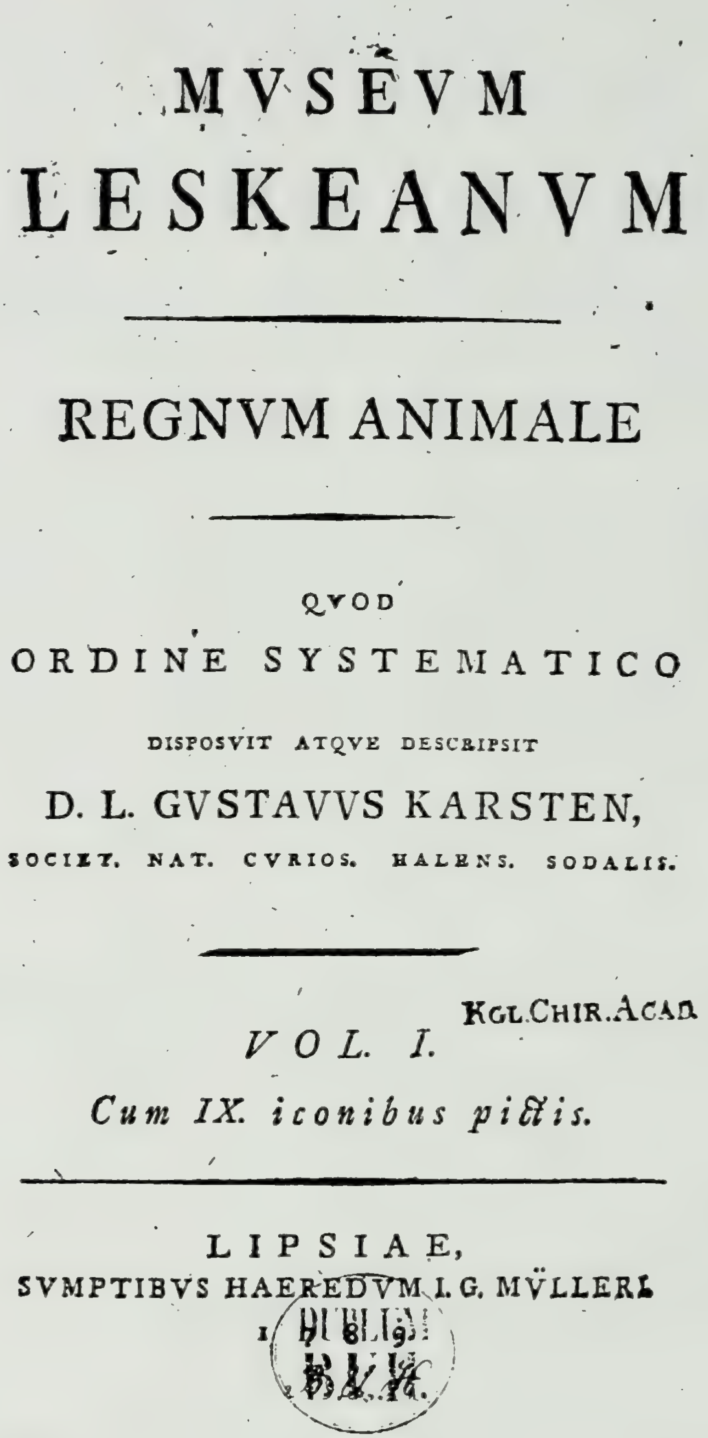

MVSEVM
LESKEANVM

REGNVM ANIMALE

QVOD
ORDINE SYSTEMATICO
DISPOSVIT ATQVE DESCRIPSIT
D. L. GVSTAVVS KARSTEN,
SOCIET. NAT. CVRIOS. HALENS. SODALIS.

VOL. I.
Cum IX. iconibus pictis.

LIPSIAE,
SVMPTIBVS HAEREDVM I. G. MVLLERI.
1789.

Fig. 1. The cover page of the *Museum Leskeanum*.

CLASSIS V.

INSECTA.

CURA J. J. ZSCHACHII.

Haec claſſis a Clariſſ. J. J. Zſchachio Med. Bacc. elaborata, jam ante annum et quod excurrit ſub titulo: Muſeum N. G. Leskeanum. Pars entomologica, ad ſyſtema entomologiae Cl. Fabricii ordinata 8 maj. in bibliopolio Mulleriano typis expreſſa eſt. Quae entomologica collectio, cum ſingularem collectoris curam expoſcat, fortaſſis a reliquo muſeo ſejuncta, naturae ſcrutatori, cuius imprimis interſit, iſtam poſſidere, ſeparatim divendetur.

Fig.2. The cover page of the part on insects

252 MUS. LESK. REG. ANIM.

Murex Olearium.

Linn. S. N. Gen. 325. Sp. 530.
a Born. teſt. muſ. Vind. pag. 297.

919 M. Ol. teſta pallida transverſim ſtriata, *ocellis ferrugineis* ſeriatim cincta, apertura dentitulata.
Chemn. Konch. Kab. T. 4. tab. 127. fig. 1223.
Long. 6 poll. 6 lin. lat. 3 poll. 8 lin.

920 M. Ol. teſta *ſubſerruginea* albido maculata, *varicibus alternis tuberculatis;* apertura lactea ad labrum incarnata fuſco maculata, labioque fuſco.
Long. 6 poll. lat. 3 poll.

921 M. Ol. teſta albida unicolor; labrum dentibus *ſolitariis* obſitum; paullulum deſtructum.
Long. 5 poll. 8 lin. lat. 2 poll. 6 lin.
Not. Hac in ſpecie plane ſecuti ſumus Perill. a Bornium; nulla enim habita ratione ſententiae Chemnitzii ſecundum quam fig. ſupra citata M. Olear. Linn. propterea non reſponderet, quod *apertura eſſet denticulata;* ſed Archiater *Linn.* etiam in Lampade, Femorali et in pluribus teſtis, aperturam *edentulam* docet, ubi Conchiologiſtae recentiores veritatem et *conſtantiam* characteris huius non confirmatam viderunt.

Cypraea amethyſtea.

Linn. S. N. Gen. 320. Sp. 334.

540 C. am. teſta ſubfuſca, antice ac poſtice *violaceo undato.* lateribus gibbis, fuſco maculatis.
Martini Konch. Kab. T. 1. tab. 25. fig. 248.
Long. 2 poll. 5 lin. lat. 1 poll. 4 lin.

Conus Ruſticus.

Linn. S. N. Gen. 319. Sp. 306.

463 C. R. teſta ex livido flaveſcens albida, in medio *faſciata,* area poſtica punctis albidis elevatis in ſeriebus cincta. Ind. Occ.
Martini Konch. Kab. T. 2. tab. 63. fig. 694.
Long. 1 poll. 8 lin. lat. 1 poll.

464 C. R. teſta *ſublivida*, apertura intus gibboſa.
Long. 1 poll. 7 lin. lat. 11 lin.

465 C. R. teſta livida albo faſciata, area poſtica *undique filis granuloſis*, antica duobus tantum cincta.
Long. 1 poll. 2 lin. lat. 9 lin.

466 C. R. teſta *flaveſcens* faſcia albida in medio *nulla.*
Long. 1 poll. 5 lin. lat. 11 lin.

Fig. 3. Examples of descriptions of mollusc species

The Family Triphoridae (Mollusca, Gastropoda) in Cuba. 4. The genera *Monophorus*, *Nototriphora*, *Cosmotriphora* and *Cheirodonta*, with the description of three new species

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KEYWORDS: Triphoridae, Caribbean Sea, Cuba.

PALABRAS CLAVE: Triphoridae, Mar Caribe, Cuba.

ABSTRACT. New information on the species known of the genera studied are reported. One new species of the genus *Monophorus* and two of *Cheirodonta* are described.

RESUMEN. Se realizan nuevas aportaciones a las especies ya conocidas de los géneros estudiados y se describen tres especies nuevas, una del género *Monophorus* y dos de *Cheirodonta*.

INTRODUCTION

Following the publication of the first works on the family Triphoridae in Cuba, in which the species of the genera *Metaxia* Monterosato, 1884 (ROLAN & FERNANDEZ-GARCES, 1993a), *Iniforis* Jousseaume, 1884 (ROLAN & FERNANDEZ-GARCES, 1993b) and *Isotriphora* (ROLAN & ESPINOSA, in press) were studied, we continue the revisory present work in which four genera are studied. New information on some of the previously known species is reported and three species new to science are described.

Additional material was recently examined from Bahamas Islands loaned by Colin Redfern, of Boca Raton, Fla. USA.

Abbreviations:

MNCN: Museo Nacional de Ciencias Naturales, Madrid
IES: Instituto de Ecología y Sistemática, La Habana
AMNH: American Museum of Natural History, New York
BMNH: The Natural History Museum, London
MNHN: Museum National d'Histoire Naturelle, Paris
ZMA: Zoologisch Museum, Amsterdam

RESULTS

SUBFAMILY TRIPHORINAE
Gray, 1847

Genus *Monophorus* Grillo, 1877

Monophorus olivaceus (Dall, 1889)
(Figs. 1-3, 6, 8, 30 MO)
= *ornatus* auct. non Deshayes, 1832

Material examined. NORTH OF CUBA: 3 specimens and 2 shells at 3 m, off the Hotel Comodoro, La Habana; 3 shells at 4 m, Jibacoa; 2 shells at 3 m, Baracoa. SOUTH OF CUBA: 6 shells at 17 m, Punta Pedernales; 4 shells at 15 m, Cayo Matías; 3 fragments at 15 m, Cayo Avalos, Archipiélago de Los Canarreos; 2 specimens and 16 shells at 3 m, Rancho Luna; and 20 shells and some fragments at 45 m, Cienfuegos Bay.

Description

Shell (Fig. 1-3) sinistral, oval-elongated with pointed apex and two or three nodulous cord on each whorl, the nodules being white or brown.

Protoconch (Fig. 6) of dark brown colour with three and a half whorls. On the first whorl there are tubercles with arrow-head shape. The other whorls have two spiral cords which are crossed by uninterrupted axial striae.

Teleoconch with about 10-12 whorls in larger specimens. The first whorls have two spiral cords from the beginning and, around the fifth or sixth whorl, a third cord begins between the previous two. This last cord is narrower, but it increases gradually to be similar to the lower one around the tenth whorl. Large and round nodules appear in the intersections of the axial ribs with the spiral cords. The colour is brown and white, the subsutural cord being brown with one white nodule between each two or three brown ones. The lower cord is always white. The intermediate cord has some white nodules and some brown. Under magnification, a very fine axial striation in the spaces between the cords and the ribs may be seen. Dimensions: the biggest shells can reach as much as 10 mm.

Animal a little translucent with variously sized spots formed by very small points of white-milk colour. The propodium has a yellowish colour marked in the anterior border of the foot.

Radula (Figs. 8 and 30 MO) with formula 15-1-1-1-15. The rachidian tooth has five cusps of similar size. The lateral tooth is very similar. The marginal teeth also have five cusps but the most peripheral have the external cusps shorter than the internal.

Remarks. FABER & MOOLENBEEK (1991) consider that the correct name for this species should be *Cosmotriphora olivacea* (Dall, 1889) instead of "*Triphora*" *ornata* Deshayes, 1832. Its position in the genus *Cosmotriphora* seems not adequate according to the characteristics of protoconch and radula: hemispherical tubercles in the protoconch and three cusps in the marginal teeth, in *Cosmotriphora*. In contrary to the other known species of *Monophorus*, the present one has an animal without red colour However, for this reason we do not think that it should be placed in another genus and we agree with the opinion of BOUCHET (1984) on the generic value of the radula and protoconch in *Monophorus*.

Monophorus ateralbus n. sp.
(Figs. 4, 5, 7, 9, 30 MA)

Material examined. NORTH OF CUBA: 2 specimens at 2 m, Marianao Beach, and 7 shells at 4 m, off the Hotel Comodoro Beach, La Habana. SOUTH OF CUBA: 2 shells and 4 fragments with protoconch at 15 m, Cienfuegos Bay. BAHAMAS: 1 shell in beach drift, Abaco Island.

Description

Shell (Fig. 4-5) sinistral, with an oval-elongated form, a little wider near the base and with pointed apex.

Protoconch (Fig. 7) with four whorls and of uniform dark brown colour. The first whorl has T-form tubercles. The others have two spiral cords crossed without interruption by axial threads, which are a little irregular and slightly oblique in some parts.

Teleoconch with 7-9 whorls, which begins with two nodulous, spiral cords. These nodules are a little bigger in the lower cord. Around the sixth to seventh whorls a new spiral cord appears, situated near the upper one. In the body whorl, at the begining, there are five nodulous cords, and near the anterior end, new spiral cords appear, there being eight by the end of the shell. Among these eight, the lower one is smaller, not nodulous and very close to the siphon. The aperture is rounded and the anal sinus is only slightly deeper but open. The siphonal canal is short, curved and closed by a fold from the external lip. The distribution of the dark brown and white colour in the teleoconch is in bands. The lower nodulous cord is white and the others are brown. This white nodulous cord ends in the anal sinus.

Dimensions between 3 and 6 mm, but the exact size of most of the collected specimens is difficult to determine because the shells with completed development of the body whorl are frequently decollated.

The **animal** has a whitish colour with numerous red-brown spots on the head and on the dorsum of the foot. The tentacles have very small white dots. There is a bigger white spot behind the head and additional spots on the posterior part of the foot. Laterally on the base of the tentacles, at the same level of the eyes, there is a small lateral prominence.

Radula (Figs. 9 and 30 MA) with formula 6-1-1-1-6. Rachidian tooth with five cusps from which two are longer. The lateral tooth has five cusps the smaller being most external. Marginal teeth have four cusps which are a little longer in the outermost ones.

Type material. Holotype (of 3.9 mm), MNCN, n° 15.05/11141; 1 paratype in IES, AMNH n° 226469, ZMA and 4 in the collections of R. Fernández-Garcés and E. Rolán.

Type locality: Marianao Beach, La Habana (Cuba).

Etymology. The specific name is due to the dark brown (almost black) and white banded coloration of the shell.

Remarks. *Monophorus ateralbus* n. sp. has a shell with brown and white spiral cords. Because of this kind of coloration, the shell must be compared with the following species: *Monophorus olivaceus* (Dall, 1889) has the spiral cords with the same colours but in each cord the nodules may be brown or white; also

different are the animal coloration and the radula. "*Triphora*" *intermedia* (C. B. Adams, 1850) has smaller and more numerous nodules and three spiral cords from the third whorl of teleoconch. "*Triphora*" *ellyae* De Jong & Coomans, 1988 has the position of the spiral cords inverted, the upper one being white and the same occurs with "*Triphora*" *elvirae* Jong & Coomans, 1988. *Iniforis turristhomae* (Holten, 1802) has smaller nodules and a tubular anal hole far from the aperture. The differences of the shell with those of the *Cheirodonta verbernei* (Moolenbeek & Faber, 1989) and *C. decollata* n. sp. are based on the different position of the brown and white colour in the spiral cords in most parts of the teleoconch.

Genus *Nototriphora* Marshall, 1983

Nototriphora decorata
(C. B. Adams, 1850)
(Figs. 10, 14, 16, 30 ND)

Material examined. NORTH OF CUBA: 4 shells at 6 m, Jibacoa; 2 shells at 8 m, Herradura. SOUTH OF CUBA: 2 specimens and 4 shells between 4 and 20 m, Punta Francés, and 1 shell and 3 fragments between 20 and 50 m, Punta Pedernales, Isla de la Juventud; 10 shells at 15 m, Cayo Matías and 1 shell at 2 m, Cayo Diego Perez, Archipiélago de Los Canarreos; 6 specimens and 15 shells between 15 and 50 m, Cienfuegos Bay

Description

Shell (Fig. 10): see ADAMS (1850) and CLENCH & TURNER (1950). This description should be complemented by the following information:

Protoconch (Fig. 14) of brown colour. It has between four and half to five spiral whorls. The first one with hemispheric tubercles very dense, the rest of the whorls with uninterrupted axial ribs crossed by one spiral cord in the first whorls and two in the lower. Near the anterior end both cords are fused into one.

The **teleoconch** presents a very fine, spiral striation in the spaces between the axial ribs, as mentioned by BOUCHET (1984).

Animal of hyaline white colour with very small white-milk spots irregularly distributed in the head and the dorsal part of the foot. Tentacles translucid. GARCIA & LUQUE (1986) mention the presence of some red spots on the flanks near the operculum; we could not find these red spots in several animals examined. We think that it is not a constant character.

Operculum rounded, with a central nucleus and a translucent yellowish-white colour.

Radula (Figs. 16 and 30 ND) with formula 18-1-1-1-18. The rachidian tooth has three equal cusps. The lateral tooth has five cusps, of which the second one is less prominent. The first marginal tooth has four cusps, the two central ones being filiform. The rest of the marginal teeth have three cusps the central one being longer and narrower.

Remarks. Some shells collected in Cienfuegos present a violet coloration instead of brown, alternating with white. As we can not find any other differences, this coloration must be considered as an ecological variation.

Genus *Cosmotriphora*
Olsson & Harbison, 1953

Cosmotriphora melanura
(C. B. Adams, 1850)
(Figs. 11, 25, 26, 30 CM)

Material examined. NORTH OF CUBA: 5 shells at 10 m, Herradura; 5 shells at 4 m, Jibacoa; 3 shells at 4 m, off the Hotel Comodoro Beach, La Habana; 2 shells at 6 m, Baracoa. SOUTH OF CUBA: 6 shells between 8 and 17 m, Cayo Matías, Archipiélago de Los Canarreos; 4 shells at 50 m, Punta Pedernales, Isla de la Juventud; 40 shells between 10 at 20 m, Cienfuegos Bay.

Description

Shell (Fig. 11), see BOUCHET (1984). It has been figured by BOUCHET (1984, p. 36, fig. 27) and by FERNANDES & ROLAN (1986, pl. 1, fig. 1, pl. 2, fig. 1), for specimens from the eastern Atlantic. WARMKE & ABBOTT (1961, pl. 13, fig. l) and ABBOTT (1974, fig. 1132) showed Caribbean specimens. The radula is drawn in BOUCHET (1984, fig. 16). The protoconch of a shell from Cuba is represented in the Fig. 25.

Animal of opalescent whitish colour with numerous white spots which are slightly yellowish in the propodium. Behind the eyes there are subcutaneous yellow areas.

Radula (Figs. 26 and 30 CM) with formula 10-1-1-1-10. It has a rachidian tooth and very similar lateral teeth, each one with four cusps. Marginal teeth have three cusps: the inner ones have their three cusps of almost equal size, while the external ones have their lateral cusps shorter and the central one longer. In the most external, the central cusp becomes filiform.

Remarks. This species is variable in size: the smallest shell is only 4 mm while others can be as much as 10 mm. The normal white coloration can become cream in some specimens. The shells from the Caribbean have been compared with specimens from Ghana and Cape Verde Islands, showing small differences: in the African shells, the third spiral cord of the teleoconch begins between the 6th and 8th whorl and always has smaller nodules than those of the other cords, except in the body whorl. On the other hand, in the shells from the Caribbean, the third spiral cord begins around the 3rd whorl and, between the 6th and the 8th, it is of similar size to the other two. Nevertheless, these differences seem not enough to consider both populations in different specific position. The protoconchs are equal and the radulas, after the examination of several specimens from Cuba and Ghana, have no significant differences. So, the observation of BOUCHET (1984) in relation to the marginal external teeth is not confirmed. It is considered an amphiatlantic species.

Cosmotriphora arnoldoi
Faber & Moolenbeek, 1991
(Figs. 12, 13, 15)

Material examined. 5 shells and 3 fragments at 20 m, Cienfuegos Bay.

Description

Shell, see FABER & MOOLENBEEK (1991). In the Figs. 12 and 13 shells are shown with normal colour distribution which was not evident in original figures because a SEM-photograph was used. Dimensions: although the holotype is of a size smaller than 3 mm, some shells from our material reach 6 mm and have 10 whorls (Fig. 12).

Remarks. In FABER & MOOLENBEEK (1991) the assignation of this species to the genus *Cosmotriphora* is not explained. Perhaps it could be on similarity of its protoconch with that of *Cosmotriphora melanura*. The lack of knowledge about the radula and operculum makes this assignation only a provisional effort.

Genus *Cheirodonta* Marshall, 1983

Cheirodonta verbernei
(Moolenbeek & Faber, 1989)
(Figs. 17, 18, 22, 30 CV)

Material examined. 1 specimen, 5 shells and 2 fragments with protoconch, in sediments at 25 m, Cienfuegos Bay.

Description

Shell (Figs. 17 and 18), see MOOLENBEEK & FABER (1989). Some shells of our material are similar to the description of the holotype, in which a brown colour with knobs of a lighter shade is mentioned. Other specimens have a lighter lower cord in the penultimate whorl and, in the body whorl, the upper one white.

The **protoconch** (Fig. 22), has the apex covered with hemispheric tubercles (it can be observed in the picture in spite of a fracture) and it is not smooth, as is mentioned in the description of the holotype, which has this part polished by erosion.

Animal translucent white with milk-white spots irregularly distributed on the dorsum.

The **radula** (Fig. 30 CV), studied from one live collected specimen and partially destroyed during the protographic process, showed a rachidian tooth with two cusps at each side and a lateral tooth with shortish cusps.

The **operculum** is rounded, light yellow, translucent, with a central nucleus, the external border obliquely elevated outwards and with a small depression in the centre of the internal part.

Remarks. The inclusion of this species in the genus *Cheirodonta* is based on the radular characteristics, similar to the *Cheirodonta labiata* (see MARSHALL, 1983, fig. 8 C) and *C. pallescens* (see BOUCHET, 1984, fig. 10-11).

Cheirodonta decollata n. sp.
(Figs. 19, 20, 21, 23, 24, 30 CD)

Material examined. NORTH OF CUBA: 8 specimens at 2 m, Marianao Beach, and 1 specimen at 3 m, Marina Hemingway, La Habana; 1 specimen and 6 shells at 3 m, Baracoa. SOUTH OF CUBA: 8 specimens and 10 shells at 3 m, Rancho Luna, 1 specimen, Cable Inglés and 8 shells at 10 m, Cienfuegos Bay.

Description

Shell (Figs. 19, 20 and 21) sinistral, ovoid-elongated, slightly pyriform, usually with the protoconch lost (only present in 1/6 of the shells studied).

Protoconch (Fig. 23) with about four whorls. The first whorl is covered by hemispheric tubercles; the rest have two spiral cords crossed by axial ribs. Dark brown colour.

Teleoconch with seven or eight whorls which present two spiral cords with rounded and rather big nodules, being slightly larger in the upper cord. On the last whorls these cords are separated, especially in the penultimate one.

In the beginning of the body whorl there are five cords, a new one appearing below the upper one. At the end of the spire there are seven or eight cords by the presence of several others. The axial ribs between the nodules are a little oblique, being more evident in the lower whorls. Towards the end of the body whorl the axial ribs are slighter and more closed; at the same time, the spiral cords are finer, bifurcated and attenuated, almost disappearing near the free border. The aperture has the form of an inverted arc; the anal sinus is deep but open. The siphon is short, curved and closed by a fold of the external lip. There is a microsculpture of microscopic tubercles spirally aligned. The coloration is very characteristic and constant: the two first whorls of the teleoconch are of a cream colour but with the subsutural cord brown. From the second whorl, both nodulous cords change to uniform brown, but from the 5th whorl can be observed that the nodules of the upper cord are slightly bigger and whitish. This white colour is more evident in the penultimate whorl. In the body whorl the upper cord is bifurcated, a finer cord appearing below. The colour of the upper cord continues white until the end where its nodules are smaller and brown, finishing in the anal sinus. The base is brown.

Animal translucid white with opaque spots formed by very small white-milk dots. Tentacles translucid.

Operculum white, translucid, multispiral and with a central nucleus.

Radula (Figs. 24 and 30 CD) with formula 7-1-1-1-7. Rachidian tooth with 9 cusps of which the central one is shorter. Lateral tooth with 8 shortish cusps. Marginal teeth of comb-like form with elongated cusps.

Dimensions. The holotype is 3.95 mm of length. Other specimens with protoconch are slightly smaller. In most shells it is not possible to know the real size due to their decollation.

Type material. Holotype of 3.95 mm and one paratype, in MNCN nº 15.05/11142. Two paratypes each in IES, AMNH nº 226470, BMNH nº 1993062, MNHN, ZMA and 11 paratypes in the collections of R. Fernández-Garcés and E. Rolán.

Type locality. Marianao Beach, La Habana.

Habitat. On rocky bottoms, under rocks or outside of the coral barrier, under dead corals.

Etymology. The species is named after the fact that it looses its apex during maturity.

Remarks. The shell of *Cheirodonta decollata* n. sp. at a superficial look may remind one of *Monophorus ateralbus* n. sp. but this last species has the lower cord white instead of brown. Also there are differences in the microsculpture of the protoconch and the radula when these characters can be studied. From *Cheirodonta verbernei* (Moolenbeek & Faber, 1989) it must be differentiated because this latter species has the first whorls of the teleoconch of uniform brown colour instead of cream with a brown cord. Also, *C. verbernei* has the lower cord white in the penultimate whorl, and the white colour of the nodules is less evident.

This species was also collected in Bahamas (Redfern, pers. com.).

Cheirodonta apexcrassum n. sp.
(Figs. 27, 28, 29)

Material examined. NORTH OF CUBA: 4 shells and 9 fragments with protoconch, in sediments at 7 m, Jibacoa. BAHAMAS: 3 shells at 10 m, Chub Rocks, Abaco Island.

Description

Shell (Figs. 27 and 28) sinistral, ovoid-elongated, a little pyriform.

Protoconch (Fig. 29) relatively large, with uniform brown colour. It begins with a well-differentiated nucleus in a vertical position, and consists of between 2 and 2 1/2 spiral whorls. These whorls present two prominent spiral cords which are irregular at the beginning and nodulous after. Another small cord is on the suture. At the end of the protoconch both cords are fused in one. The beginning of the teleoconch is ill-defined.

Teleoconch with 5-6 whorls. It begins with the lower cord a continuation of the only cord of the protoconch. Later, the upper cord appears smaller, but increasing quickly and achieving the same size as the lower one. Both have evident nodules which are connected by axial ribs. Towards the fourth whorl a new cord appears between the last ones, nearer the upper one and with smaller knobs. On the body whorl there are six cords from which the three upper ones are nodulous, the three lower being smooth. Aperture slightly ovoid with a prominent cutting external lip and a superior open anal sinus. In the base there is a fold which closes the siphonal canal. The siphon is short and curved. The columellar lip has a basal prominence towards the beginning of the siphonal canal and another up near the sinus. Coloration is almost uniform brown, the upper cord a little lighter in the last whorls and also lighter in the external lip of the aperture.

Type material. Holotype (Fig. 27) of 2.78 mm, in MNCN nº 15.05/11143. One paratype each in IES, AMNH nº 226471, BMNH nº 1993061, ZMA, MNHN and the collection of R.

Fernández-Garcés; three (from Abaco) in that of Redfern and six in that of E. Rolán.

Type locality. Jibacoa, in North of Cuba.

Etymology. The specific name makes reference to the thickness of the protoconch.

Remarks. The position of the present species in the genus *Cheirodonta* is only tentative, based on the great similarity (shell and protoconch) with the species shown by MARSHALL (1983), *Cheirodonta labiata* (A. Adams, 1851) from Australia.

Cheirodonta apexcrassum n. sp. can be differentiated from *"Triphora" calva* Faber & Moolenbeek, 1991 because this last species has a smaller protoconch and smaller nucleus; also lacks the two constant cords of the protoconch. It differences from the other species of the genus described in the present work by having a paucispiral protoconch.

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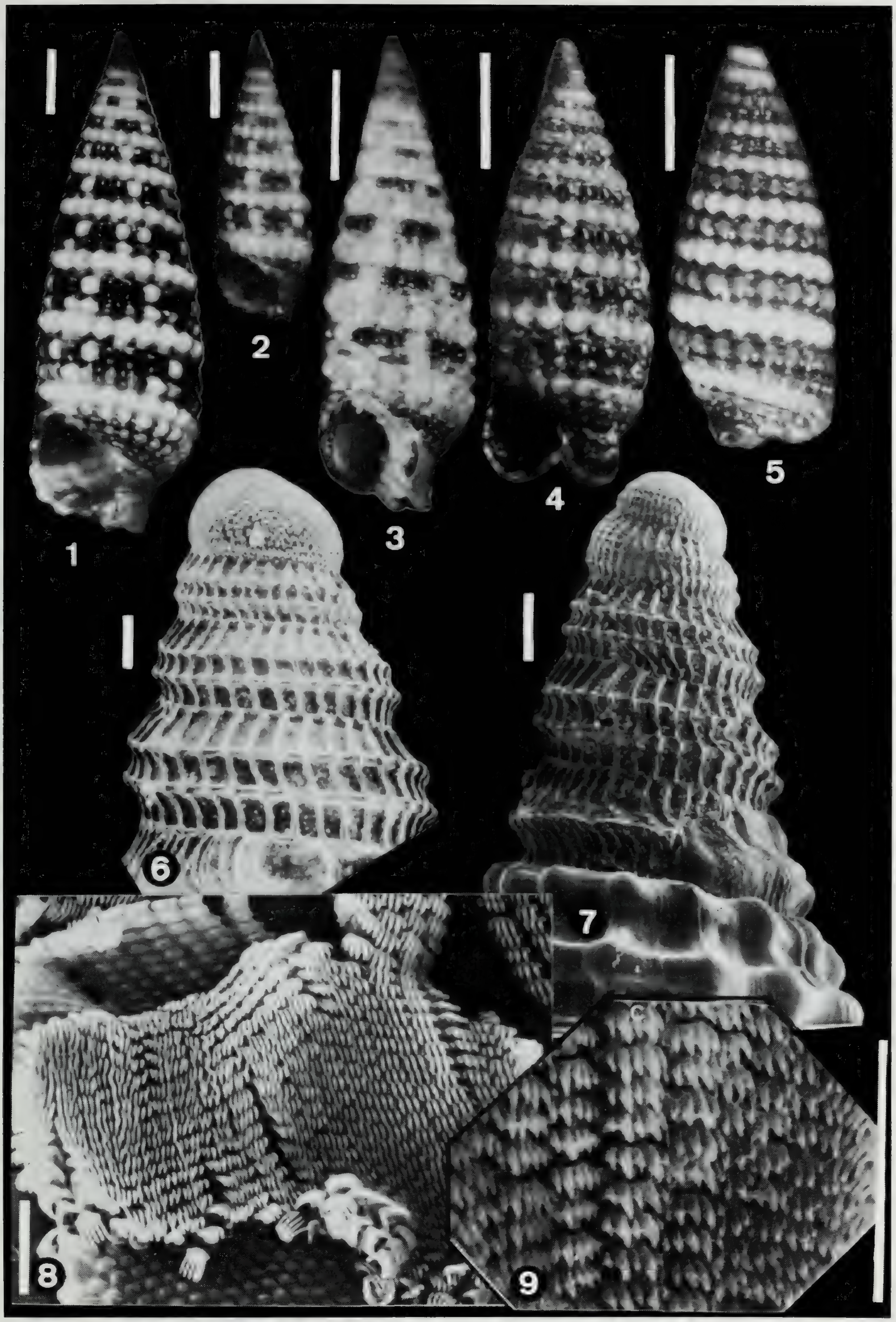
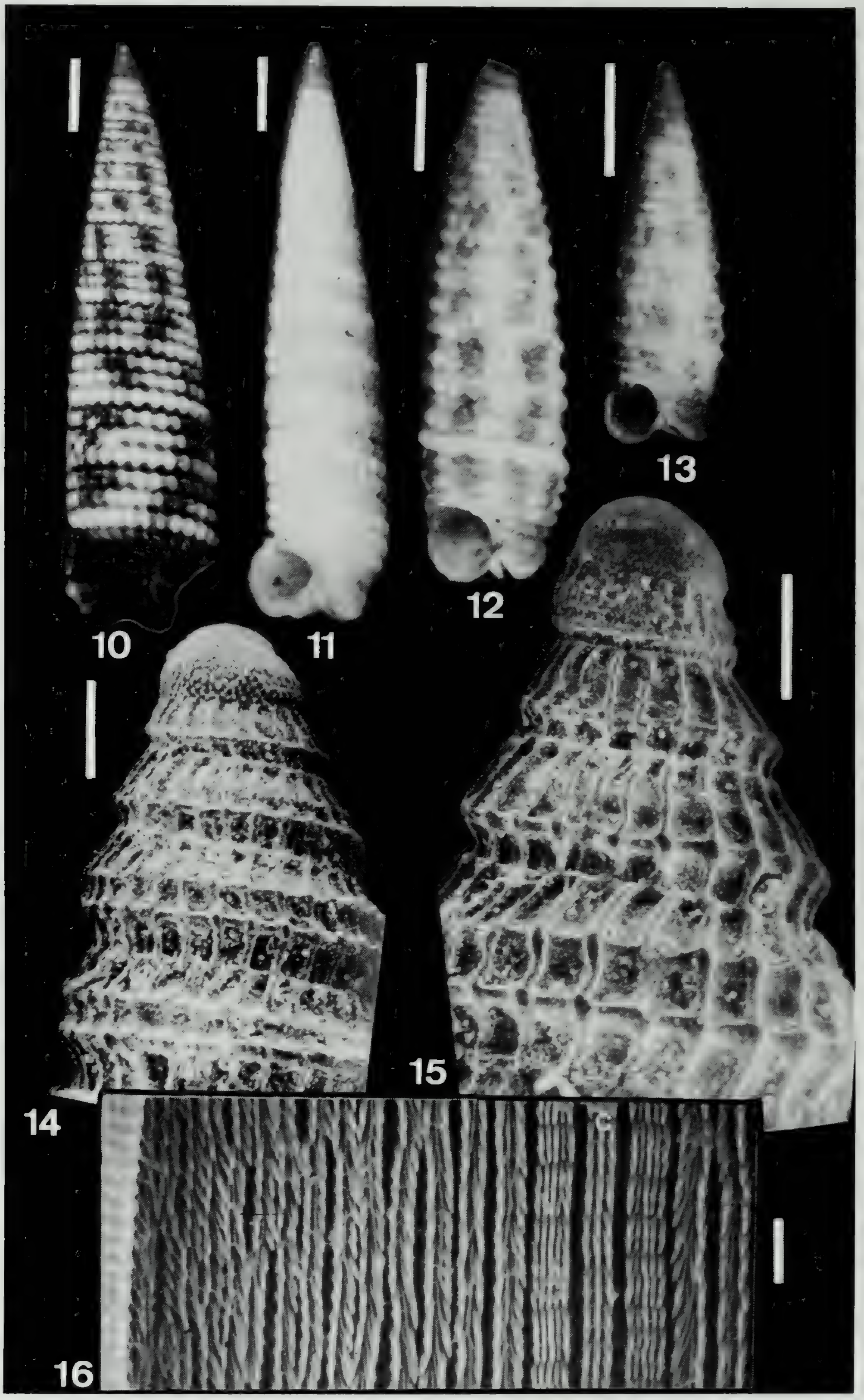
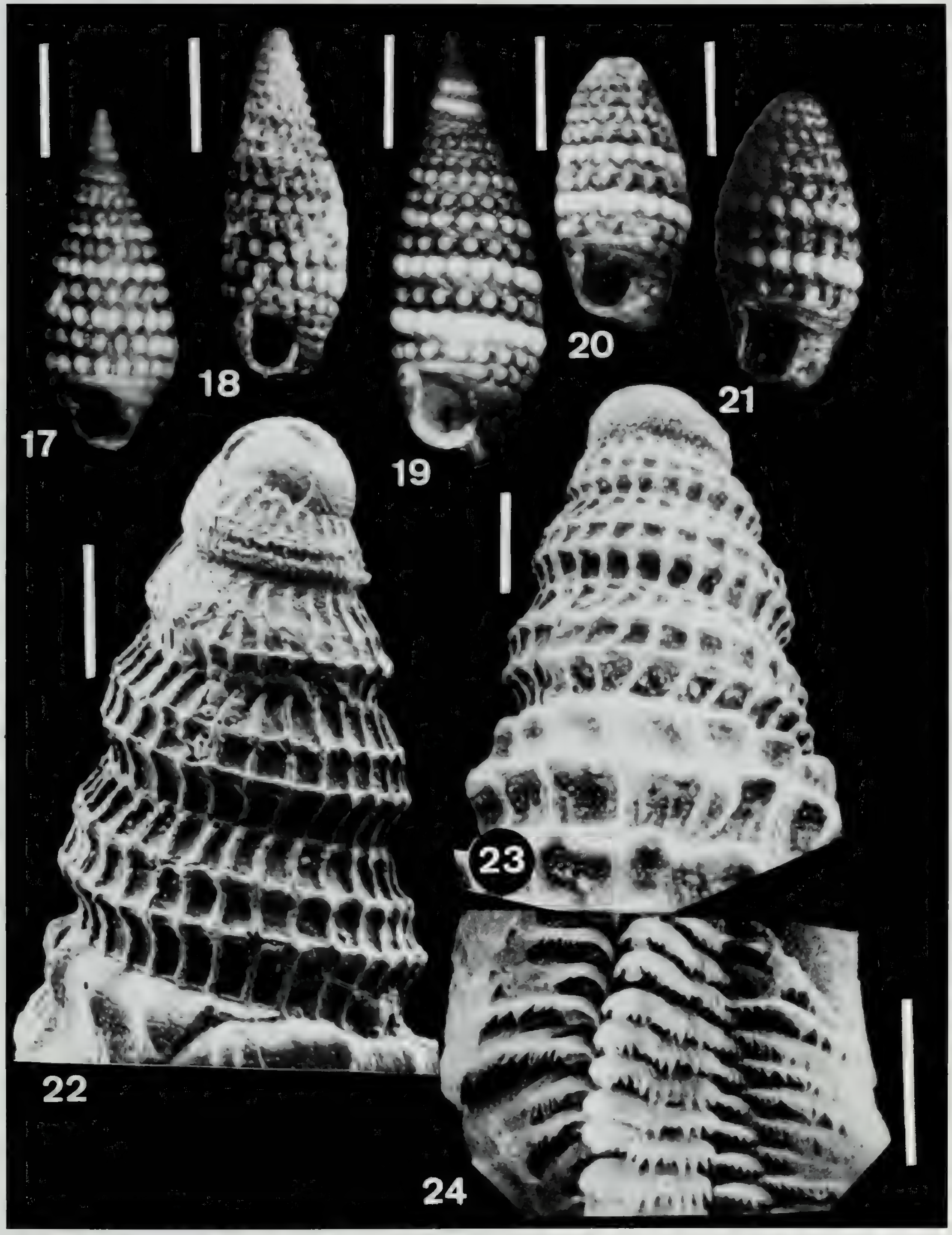


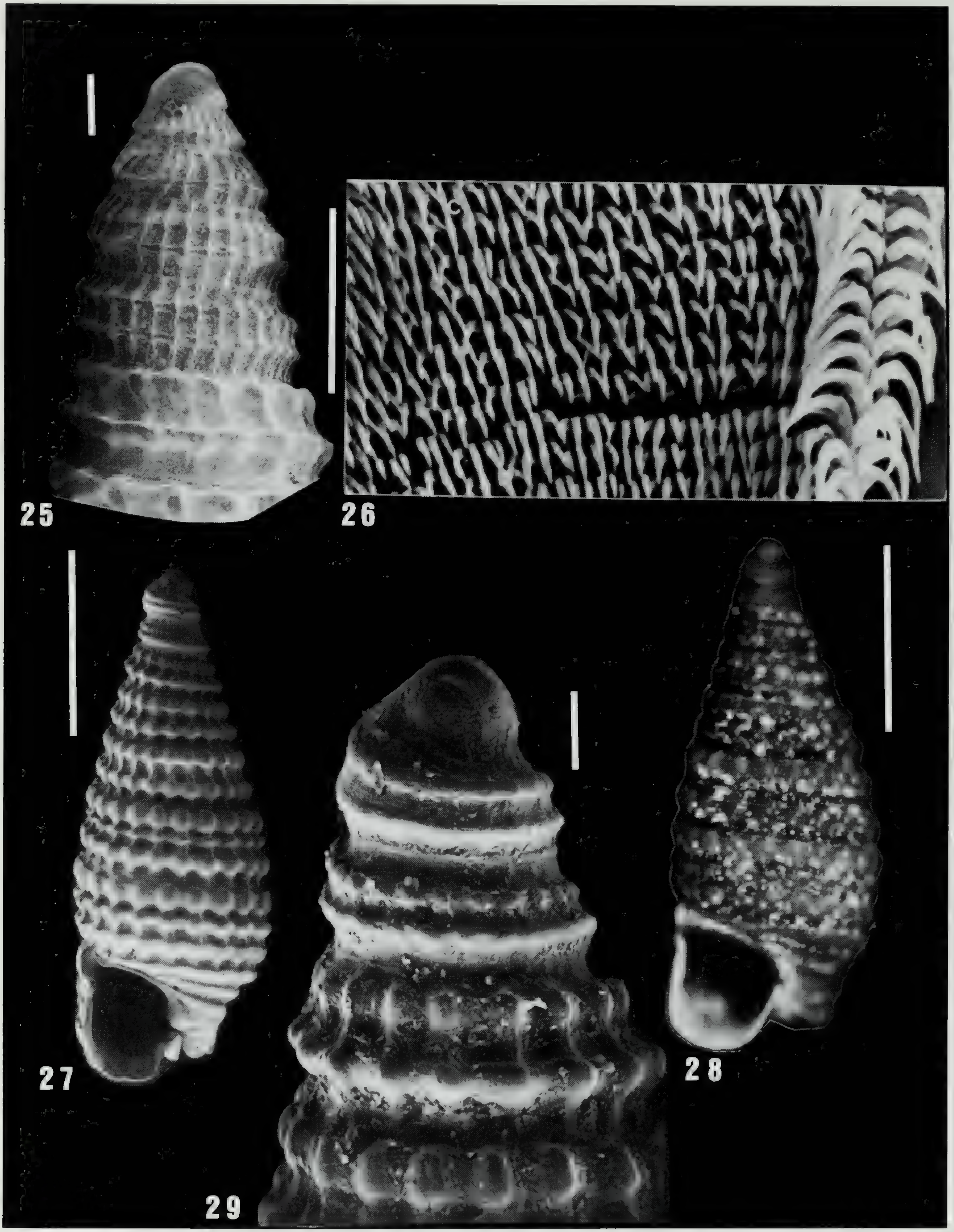
Figs. 1-9.
1-3. *Monophorus olivaceus*; 4. *Monophorus ateralbus* n. sp. Holotype (MNCN);
5. *Monophorus ateralbus* n. sp. Paratype (coll. E. Rolán); 6. *Monophorus olivaceus*. Protoconch; 7. *Monophorus ateralbus*. Protoconch; 8. *Monophorus olivaceus*. Radula.
9. *Monophorus ateralbus* n. sp. Radula.
(scale bar: shells: 1 mm; protoconchs: 0.1 mm; radulas 0.01 mm)



Figs. 10-16.
10. *Nototriphora decorata*; 11. *Cosmotriphora melanura*; 12. *Cosmotriphora arnoldoi*; 13. *Cosmotriphora arnoldoi*; 14. *Nototriphora decorata*. Protoconch; 15. *Cosmotriphora arnoldoi*. Protoconch; 16. *Nototriphora decorata*. Radula.
(scale bar: shells: 1 mm; protoconchs: 0.1 mm; radulas 0.01 mm)



Figs. 17-24.
17-18. *Cheirodonta verbernei*; 19. *Cheirodonta decollata* n. sp. Holotype (MNCN).
20-21. *Cheirodonta decollata* n. sp. Paratypes (col. E. Rolán); 22. *Cheirodonta verbernei*. Protoconch; 23. *Cheirodonta decollata* n. sp. Protoconch; 24. *Cheirodonta decollata* n. sp. Radula.
(scale bar: shells: 1 mm; protoconchs: 0.1 mm; radulas 0.01 mm)



Figs. 25-29.
25. *Costrotriphora melanura*. Protoconch; 26. *Costrotriphora melanura*. Radula. C central tooth; 27. *Cheirodonta apexcrassum* n. sp. Holotype (MNCN); 28. *Cheirodonta apexcrassum* n. sp. Paratype (Col. E. Rolán); 29. *Cheirodonta apexcrassum* n. sp. Protoconch. (scale bar: shells: 1 mm; protoconchs: 0.1 mm; radulas 0.01 mm)

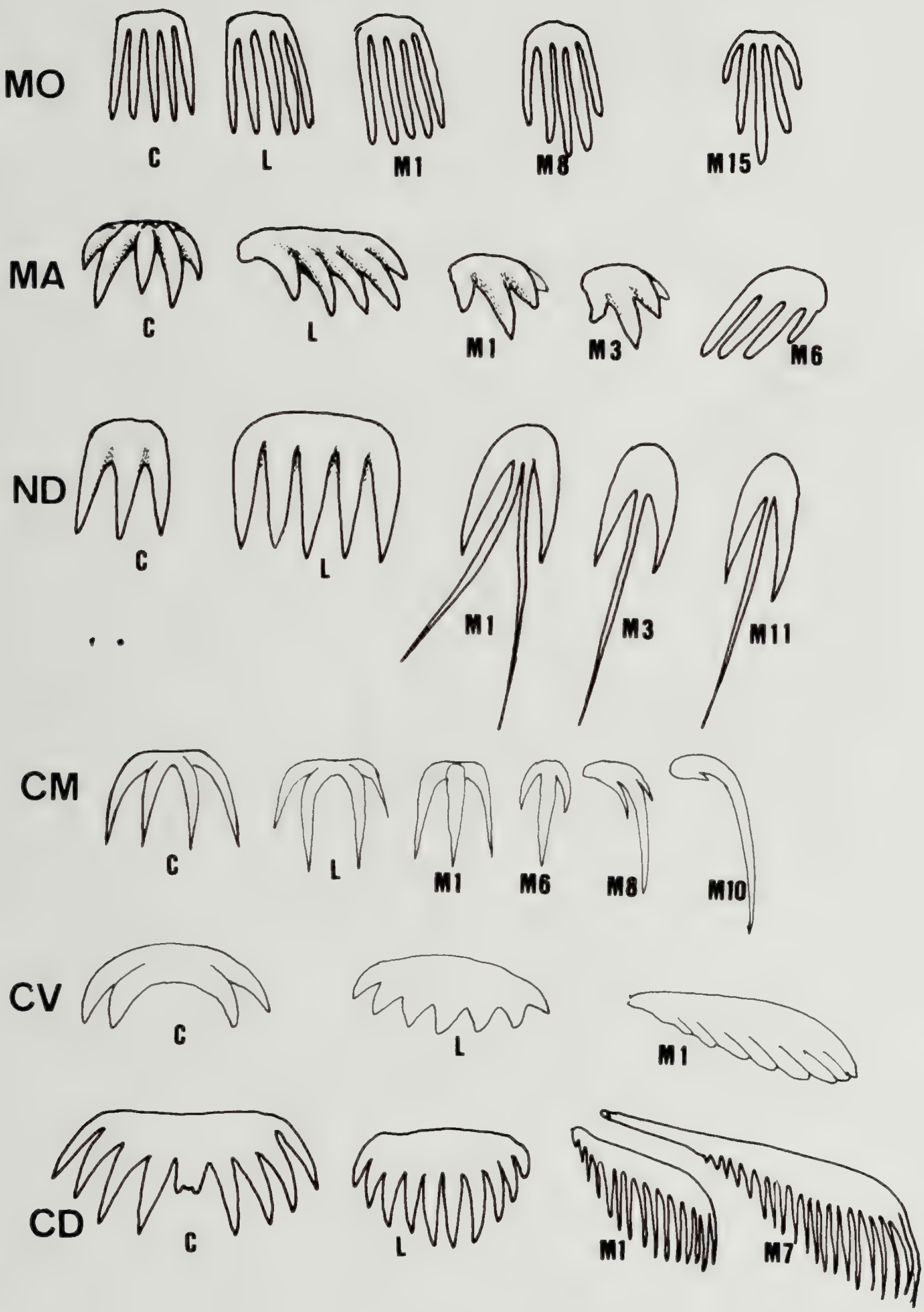


Fig. 30.- Radular teeth:
MO: *Monophorus olivaceus;* MA: *Monophorus ateralbus;* ND: *Nototriphora decorata*
CM: *Cosmotriphora melanura;* CV: *Cheirodonta verbernei;* CD: *Cheirodonta decollata*
C- rachidian tooth; L- lateral tooth; M1-2-etc.- marginal teeth.

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Studies on Olividae. XVIII. The distribution of *Oliva* species and the variation of their colour patterns in Hansa Bay (Papua New Guinea).

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ABSTRACT. Sediments of 64 stations where *Oliva* species have been collected in Hansa Bay (Papua New Guinea) have been analysed for carbonates, organic carbon and granulometry. Comparison between the classification of sediments and the distribution of 30 species shows that the latter fall into stenotopic and eurytopic species. Crypsis is generalised in both groups of species. The taxonomic consequences of crypsis are discussed.

RESUME. Les sédiments de 64 stations auxquelles des espèces d' *Oliva* ont été récoltées dans Hansa Bay (Papouasie Nouvelle-Guinée) ont été analysés pour leur teneur en carbonates, en carbone organique et leur granulométrie. La comparaison entre la classification des sédiments et la distribution de 30 espèces montre que ces dernières se divisent en espèces sténotopiques et eurytopiques. La crypsis est généralisée dans les deux groupes. Les conséquences taxonomiques de la crypsis sont discutées.

KEYWORDS. Mollusca, Gastropoda, *Oliva*, habitat, sediments, stenotopy, eurytopy, crypsis, polymorphism, taxonomy.

1. INTRODUCTION.

1.1. The problem.

One of the main biological causes of the old "*Oliva* problem" is the great variability of their colours and colour patterns. Colour variations said to be habitat-related have been observed by field collectors (such as HAMLYN-HARRIS, 1970) and the possibility that some described "species" could be ecovariants (GREIFENEDER, 1981) or colour morphs (PETUCH & SARGENT, 1986) has been raised. So the topic of habitat does not only concern ecology and ethology; it also has taxonomic implications.

1.2. Colour variation in molluscs.

A great number of studies (see ETTER, 1988) have been prompted by the obvious variations in the shell pigmentation of some molluscs. Much caution is necessary in the interpretation of such data. Many factors -such as the influence of environmental factors (COLTON, 1916; CREESE & UNDERWOOD, 1976; ETTER, 1988; MITTON, 1977), food (COLE, 1975; INO, 1949; LEIGHTON, 1961; MOORE, 1936), genetic determinism (ADAMKIEWICZ & CASTAGNA, 1988; INNES & HALEY, 1977; PALMER, 1985), selective predation (ELEK & ADAMKIEWICZ , 1990; REIMCHEN, 1979), behavioural polymorphism (GIESEL, 1970) and combinations of these can be (and have been) invoked to account for the observed facts.

The classical example of colour polymorphism in terrestrial molluscs populations is that of *Cepaea nemoralis* (CAIN & SHEPPARD, 1954; LAMOTTE, 1959; MURRAY, 1962; JONES *et al.* 1977) where the relative proportion of genetic morphs varies with habitat, even in localities separated by short distances and this has been correlated with the ability of a predator (thrushes, in that case) to detect their prey. Another visual predator, man, was shown to be responsible for the maintenance of colour polymorphism in an unidentified African Achatinid snail (OWEN & REID, 1986).

Contribution n° 285, Station Biologique Léopold III, Laing Island, Papua New Guinea.

Conflicting interpretations have been proposed for some species. The degree of pale striping in the shell of the blue mussel *Mytilus edulis* was interpreted as having an adaptive significance, the morphs varying in the proportion of incident sunlight transformed into heath (MITTON, 1977). On the contrary, INNES & HALEY (1977) concluded that the coloration polymorphism of *Mytilus edulis* was determined by genetic rather than by environmental differences. Colour changes associated with a change of food were first reported for *Nucella lapillus* by MOORE (1936), after COLTON (1916) noted that the shell colour of this mollusc was influenced by the environment. It was later shown that the interpopulation variation in shell colour of *Nucella lapillus* is in part a response to a selective gradient in the physiological stress due to temperature and desiccation and that selection for crypsis by visually hunting predators does not appear to play a prominent role (ETTER, 1988).

In summary, the better studied cases in marine molluscs point at an "*intimate relationship between genotypic and environmental factors which influence prosobranch shell colour*" (COLE, 1975).

The enormous number and variety of colour forms in some natural populations could be an adaptation in itself, providing protection against visual predators. This hypothesis, known as reflective selection was proposed by MOMENT (1962) for extremely variable *Donax* species.

1.3. Purpose.

Any attempt at defining a potential correlation between the colour pattern of *Oliva* specimens and their habitat had to start with the accumulation of detailed habitat data. Very little detailed information on the habitat of *Oliva* species is available, excepted for a few qualitative reports (HEMMEN, 1981; WIDMER, 1981; WITTIG-SKINNER, 1981).

It was felt that useful information could be gained by a methodical study of the distribution of a number of *Oliva* species between different, well-characterised sediments within a restricted geographic range, followed by the analysis of a possible habitat-pattern relationship.

1.4. Location.

A most suitable location for such a study is provided by Hansa Bay, on the North coast of Papua New Guinea. It is a small semicircular bay (approximately 10 km in diameter) located in Madang Province, near the mouth of the Ramu River, about 110 nautical miles West of Madang. Laing Island (4°10'30"S - 144°52'47"E), lying roughly at the middle of the bay is a raised coral reef, covered with vegetation and separated from the mainland by depths of 45-50 m, muddy bottom. Climatic and hydrological data are described by BOUILLON *et al.* (1986) and CLAEREBOUDT *et al.* (1989). Detailed environmental data can be found in CLAEREBOUDT (1989). All the coast of Hansa Bay is lined with a long black sand beach, except for small Boro Beach that is formed of white, coarse coral sand.

2. MATERIAL AND METHODS.

2.1. The collection of *Oliva*.

The *Oliva* species of Hansa Bay have been under survey for nearly 20 years, since the establishment of King Leopold III Biological Station on Laing Island in 1974.

Oliva specimens have been obtained over the years by a variety of methods including dredging (using a small rectangular steel mesh dredge with an opening of 60 x 22 cm), trawling (with a small mesh 3 m rigid frame trawl), SCUBA diving (day and night dives), snorkelling in shallow waters, or beach collecting at the turn of the low tide. When diving, small rigid steel mesh hand "dredges" (in the shape of a dustpan, about 20 x 30 cm) have been especially productive. Baiting and trapping have been often used.

The 30 following species have been collected in Hansa Bay: *O. amethystina* (Röding, 1798), *O. athenia* Duclos, 1835, *O. buelowi* Sowerby, 1888, *O. bulbiformis* Duclos, 1835, *O. caerulea* (Röding, 1798), *O. carneola* (Gmelin, 1791), *O. ceramensis* Schepman, 1911, *O. concavospira* Sowerby, 1914, *O. concinna* Marrat, 1871, *O. sp. DHB* (abbreviation for species "D" of Hansa Bay), *O. dubia* Schepman, 1911, *O. elegans* Lamarck, 1811, *O. funebralis* Lamarck, 1811, *O. longispira* Bridgman, 1906, *O. mantichora* Duclos, 1835, *O. miniacea* (Röding, 1798), *O. mucronata* Marrat, 1871, *O. panniculata* Duclos, 1835, *O. parkinsoni* Prior, 1975, *O. paxillus* Reeve, 1850, *O. reticulata* (Röding, 1798), *O. rufula* Duclos, 1835, *O. semmelinki* Schepman, 1911, *O. sericea* (Röding, 1798), *O. smithi* Bridgman, 1906, *O. solomonensis* Petuch & Sargent, 1986, *O. tesselata* Lamarck, 1811, *O. vidua* (Röding, 1798), *O.* cfr. *volvaroides* Duclos, 1835, *O. sp. ZHB* (abbreviation for species "Z" of Hansa Bay).

As far as we know, this is by far the largest number of *Oliva* species ever recorded for a single locality, but this might only reflect an unusual collecting effort. Nearly all species have

been obtained in adequate numbers and most specimens have very accurate locality data. All species have been kept and observed in aquaria, some for several months.

The taxonomy of the genus *Oliva* being what it is (see ABBOTT, 1991), some of the above names will undoubtedly have to be corrected in the future. For the time being, the names *O. longispira* and *O. smithi* were selected only because of the existence of adequate type material. These two taxa are respectively the "*species L+X*" and "*species G*" of the "*Oliva oliva* complex" (see TURSCH & *al.*, 1992). *O. amethystina* and *O. mantichora* were formerly part of *O. annulata* Gmelin, 1791, a *nomen dubium* encompassing a mixture of species (TURSCH, GERMAIN & GREIFENEDER, 1986). *O. sp. ZHB* (the specific rank of which is still open to question) and *O. sp. DHB* have been collected in numbers but could not be positively identified. Decision on their taxonomic status depends upon future biometric comparison with all possibly related type material.

2.2. The analysis of sediments.

During 20 years of study, *Oliva* specimens have of course been collected at many more locations than we could analyse for sediment and representative stations had to be selected. Two maps (Figs. 1 and 2) show the points where samples were collected in the early months of 1992. Individual sampling stations can be identified in Table 1.

All sediments were collected by diving, about 800 g being taken in the first 6 cm of substrate, corresponding to the maximum observed burrowing depth observed for *Oliva* species (VAN OSSELAER & *al.*, 1993). The samples were homogenised, dried at 70-80°C in an oven at Laing Island, individually sealed and sent to Brussels for analysis. The colour of the dried sediments was determined with the Rock Colour Chart of the Geological Society of America. Each sample was separated (homogeneous fractionation by inquartor) into a fraction of about 10 g for carbon analysis and a fraction of about 100 g for granulometric analysis. All weightings were effected with a 0.01 g precision.

Granulometric analysis was effected by sieving, using the Udden scale modified by Wenthworth. Sieves were selected for the sand's range, as commonly used in studies of benthic fauna (see for instance JONES *et al.*, 1990). The samples were passed through a series of sieves (2000, 1000, 500, 250, 125 and 63 µm mesh) in a vibrating shaker (HAVER and BOEKER) for 20 minutes (15 minutes for calcareous sands that are subject to rapid mechanical wear).

For total carbon analysis, an aliquot of about 10 g of sample was finely ground in a FRITSCH apparatus (type WRR 731 1/4) for 5 min at 98 rpm. Analysis was effected by pyrogenation followed by measurement of the released carbon dioxide with a STRÖHLEIN carbon doser calibrated with Standard B.C.S. Steel 163/2. Temperature and atmospheric pressure corrections were accounted for (using the Ströhlein's "Umrechnungstabelle zum Kohlenstoffbestim-mungsapparat").

The same technique was used for organic carbon analysis, but after prior elimination of the carbonates by treating with 50% HCl until no more effervescence was observed, then drying on a hot plate. Carbonate content is calculated from the difference between the total carbon and the organic carbon.

Every sample was thus characterised (see VAN OSSELAER, 1992) by a reference number, a date and the 13 following parameters: locality, depth, colour, % total carbon, % organic carbon, % carbonates and the percentages of the seven textural classes (>2000 µm, 2000-1000 µ m, 1000-500 µm, 500-250 µm, 250-125 µm, 125-63 µm and < 63 µm).

3. RESULTS.

3.1. The classification of sediments.

The data obtained on the sediment samples are given in Table 2. Multivariate analysis soon revealed that some order was hidden in that apparent chaos.

Application of the classical U.P.G.M.A. (Unweighted, Pair-group, Method using arithmetic Averages) clustering method (see SNEATH & SOKAL, 1973) using squared Eucliduan distances to the matrix containing six textural classes, the percentage of organic carbon, the percentage of carbonates and depth yields the dendrogram shown in Fig. 3. Taking all seven classes into account would introduce redundancy, as the sum of the classes is necessarily 100%. Sediments are characterised mainly by either fine or coarse particles, so we elected to eliminate one of the 3 intermediate textural classes. Amongst these, the class 250-125 µm has the smallest contribution to the total variation (in the analysis of principal components on raw data) and was therefore discarded.

It can be seen that the sediments fall into two clusters that are very clearly separated (over 50% of the maximal distance between groups).

One of these clusters corresponds to light-coloured coral sands, with coarse particles and a high carbonate content. Colours of dry samples of this group were: bluish white 5B 9/1, dusky yellow 5Y 6/4, grayish yellow 5Y 8/4, light olive gray 5Y 6/1, very pale orange 10YR 8/2, yellowish gray and yellowish gray 5T 7/2. The other cluster corresponds to dark terrigenous sediments with fine particles and low carbonate content. Colours of dry samples of this group were: dark greenish gray, dark greenish gray 5GY 4/1, grayish olive 10Y 4/2, greenish gray 5GY 6/1, light olive gray 5Y 5/2, olive gray, olive gray 5Y 3/2 and olive gray 5Y 4/1. For the sake of simplicity we shall not use the rich vocabulary available for sediments (see for instance COLLINSON & THOMPSON, 1989) and these groups will be here under referred to as "black substrate" and "white substrate".

U.P.G.M.A. clustering works on distances in the attribute hyperspace and gives no information on the relative importance of the different factors under consideration. This was obtained by the equally classical F.A.C. (Factorial Analysis of Correspondences) method, first effected on all the factors considered in the analysis here above. The same analysis, performed with all textural classes (this hardly brings any modification in this case) is illustrated in figure 4. It fully confirms not only the existence of the two groups "black" and "white" obtained by U.P.G.M.A. but also the correctness of their interpretation. The principal axis (52.7 % of the total inertia) corresponds to the textural classes, ordered by size. The least important factors are depth and organic carbon.

The same analysis, effected without considering depth hardly shows any modification. This might appear surprising at first sight but is quite logical because organic matter is related to depth, the role of which depends upon the nature of the sediment. This is confirmed by the observation that when F.A.C. are performed separately on each group of sediments (not illustrated here), the contributions of depth and organic carbon become apparent, especially in the case of black sediments.

Very similar results were obtained by A.P.C. (Analysis of Principal Factors, not illustrated here).

The clustering of sediments into two groups can even be evidenced in a much simplified representation (Fig. 5) in which all stations are reported on a scatter diagram of the carbonate content *vs.* depth.

It must be stressed that this classification into two clear-cut, compact groups does not encompass all the sediments of Hansa Bay but only those in which *Oliva* specimens have been found. The two groups of sediments are most probably bridged by intermediate, deep water points, where *Oliva* have not been met with.

3.2. The distribution of species.

The occurrence of the various *Oliva* species at the different stations, together with a brief description of their common habitat, is given in Table 3.

3.2.1. Correlation with depth.

The distribution of the *Oliva* species in Hansa Bay is obviously related to depth, as can be seen on the graph of figure 6. Some species are restricted to deep water and some others to shallows. One will notice that the observed depth range of some species is rather extensive. Specimens of *O. amethystina, O. panniculata* and *O. paxillus* have exceptionally been collected at much greater depths than normal. These rare findings occurred only on very steep reef slopes and have not been reported in the graph, as they are most probably accidental (on such slopes, an unsuccessful attack by a predator could result in a considerable fall). With the exception of the widespread *O. carneola,* wide depth ranges seem to be a feature of deep water species.

The graph of figure 7 gives the number of species as a function of depth. The curve sharply culminates at 5m (where two thirds of the Hansa Bay species can be found) then shows a rapid, regular decrease.

The distribution of *Oliva* species is certainly not a function of depth alone. If this would be the case, all shallow water species would be expected to coexist, which is not at all the observed situation. One should be aware that the correlation between depth and distribution is most probably indirect: Olives are not known to possess any pressure-sensitive anatomical structure and specimens can be rapidly brought to the surface from -70 m, then kept for extended periods in aquaria without any apparent disability.

3.2.2. Correlation with nature of the sediment.

The distribution of each species was established by drawing contour lines around its points of presence both in the F.A.C. diagram and in the depth vs. carbonate scatter diagram. For the sake of space economy, only two species, *Oliva parkinsoni* and *O. reticulata* will

be given as examples. It can be seen (Figs. 4 and 5) that these two species have different distributions (this is also apparent on the UPGMA, Fig. 3). *O. parkinsoni* is found only in a very restricted zone of "white" sediments, while *O. reticulata* occupies disjunct portions of both "black" and "white" sediments. The following groups of species are observed:

Species found on "white" substrate only: *O. amethystina* (°), *O. buelowi*, *O. caerulea* (°), *O. concinna*, *O. mantichora*, *O. miniacea*, *O. panniculata*, *O. parkinsoni*, *O. paxillus*, *O. semmelinki*, *O. sericea* (°), *O. tesselata*. The species marked (°) are found also in small patches of somewhat darker "white" coral sand (coloured with terrigenous sediments) formed around World War 2 wrecks lying in "black" sediment.

Species found on "black" substrate only: *O. athenia*, *O. ceramensis*, *O. concavospira*, *O. sp. DHB*, *O. dubia*, *O. funebralis*, *O. mucronata*, *O. rufula*, *O. sp. ZHB*.

Species found on both "black" and "white" substrates: *O. bulbiformis*, *O. carneola*, *O. elegans*, *O. longispira*, *O. reticulata*, *O. smithi*, *O. solomonensis*, *O. vidua*, *O.* cfr. *volvaroides*.

The species restricted to only one type of sediment will be here under referred to as *stenotopic* and the species occupying different types of substrate as *eurytopic*. Experiments in aquaria (VAN OSSELAER & *al.*, 1993) have shown that it is highly unlikely that restriction of habitat is caused by a choice of substrate by adult specimens.

3.3. Observations on colour patterns and crypsis.

Oliva species are famous for the variability of the colour pattern of their shells, but this variability is not entirely haphazard. Our observations fully confirm the previous impressions that the colour pattern can vary with the substrate. Of the 30 *Oliva* species collected in Hansa Bay 28 are cryptic (coloration and markings of the shell and the soft parts resemble the surroundings and aid in concealment). For instance *O. amethystina* and *O. mantichora* that live exclusively in coral sand in proximity to live reefs, are easily mistaken for fragments of dead *Acropora* coral. The crypsis of more colourful species like *O. semmelincki*, *O. parkinsoni* and the brightly coloured *O. buelowi* is not evident when specimens are seen in a drawer but quite convincing in the field: these species live in much deeper water, where the colours red and orange are seen dark brown and brown. One must also remember that the sediment is generally not uniform but contains debris and rubble of various sizes. On such a substrate, the reticulated or variegated pattern of many olive shells constitutes a most effective camouflage.

One should note that in eurytopic species both the mantle and the shell are cryptic. The general aspect can vary strikingly within the same species (see Pl. 1, Figs. 6 and 7).

The two non cryptic species are *O. carneola* and *O. rufula*, which will be discussed later.

There is an obvious (and probably continuous) variation in the "*colour strategy*" of the *Oliva* species in Hansa Bay. On the one hand, for most species every local micropopulation is cryptic and quite homogeneous in colour pattern. An experienced local collector can often guess the exact origin of a given specimen because the colour pattern is often characteristic of a given locality.

On the other hand, local populations of a species can be extremely heterogeneous. Of 35 specimens of *O. concinna* (found exclusively on white sand off Boro Beach) 25 (71%) were white, 9 were all black and 1 was orange. Of nearly one thousand *O. longispira* specimens observed on the black beach at Sisimangum 76% were "black", 15 % were "white" and 9 % did not fit into these categories. In these populations, it is only the large majority of the specimens that is cryptic. These are clear cases of population polymorphism. It is interesting to note that the "colour strategy" of a given species can differ from one locality to another. We have just seen that *O. longispira* is polymorphic on the black sand of Sisimangum beach but it is not so on the white sand of Boro Beach where all of the 42 collected specimens of this species were "white". This can also be observed for *O. carneola*, some populations of which are very homogeneous while others are highly heterogeneous. Some of the homogeneous populations of this species are cryptic, others not.

Intermediate strategies do occur. For instance, the colour pattern of the *O.. vidua* populations is always cryptic but very variable within a given micropopulation.

4. DISCUSSION.

The *Oliva* species habitats reported here are based only upon observations in Hansa Bay. It is conceivable that the same species might occupy different habitats in other localities. The present data so far agree with the habitats we have observed in other localities in Papua New Guinea (Boesa I., Legoarant Is.; Bogia,

Madang, New Ireland) and in other regions of the Indo-Pacific (Indonesia, Seychelles, Sri Lanka, Thailand, Vietnam).

4.1. Crypsis.

One might wonder what olives that are burrowing and nocturnal could gain from crypsis, a strategy obviously directed at diurnal predators endowed with good vision. But olives do come in full light when they detect prey at the sediment surface (they burrow back immediately after the capture of prey). As they do not bury deep (only a few centimetres, see VAN OSSELAER & *al.*, 1993) they could also easily be exposed by any of the many digging or rummaging predators present in their biotope. Crypsis is then very efficient, especially when compounded with very fast burrowing (many a diving collector will recall a coveted *Oliva* specimen literally vanishing under his eyes). A strong argument for crypsis being due to predator pressure stems from the observation (see Plate 1) that crypsis is more convincing on the dorsal face and the mantle (the parts a predator is more likely to see) than it is on the ventral face.

In Hansa Bay, there are two exceptions to the generalised crypsis of *Oliva* species. The first is arguably *O. rufula* (Fig. 8), restricted to deep, dark, very soft sediments. Although its background colour blends with its surroundings, its strikingly disruptive colour pattern could be interpreted as an aposematic (warning, protective) signal, indeed the very contrary of crypsis. The pattern is indeed seen as very contrasting nearly black-and-white if on a colour picture of *O. rufula* one filters off the colours red and yellow (that do not reach the depth where the animal lives). This interpretation is tenable because we have often observed captive, stressed specimens of this species to produce a deep-green, highly toxic exudate.

The second, quite obvious exception is the abundant *O. carneola* (nearly ubiquitous from 0 to -30m). The populations of this very variable species are not homogeneous in coloration: those living on "black" sediment consist mostly of brownish (cryptic) specimens while populations from "white", shallow substrates consist very predominantly in bright orange individuals, sharply contrasting with their surroundings. We still lack data on the possible defences of this form (which produces a bright yellow exudate of unknown toxicity) and have no interpretation to propound for this puzzling case.

The Hansa Bay *Oliva* species display a large spectrum of "colour strategies" and strict analogy with any of the previous studies on shell colour variation (see Introduction) is not obvious. In our case the problem is even more complex because the colour pattern of *Oliva* specimens can vary during the lifetime of an individual, as attested by the abrupt colour pattern changes often observed on the shells of many species. Synchronism of such colour pattern transitions in a population of the East African *O. bulbosa*, has led GREIFENEDER (1984) to suggest that colour pattern changes could be used as a "chronicle of the habitat".

The possibility that the shell colour of *Oliva* specimens depends upon food cannot be rejected at this point. The colour of the small bivalves that seem to constitute an important part of the diet of *Oliva* species is also often matched to the colour of the sediment.

Oliva species could constitute an ideal experimental material for the study of shell colour variation, if one could solve the problem of raising their veliger larvae. These are very easy to obtain but our first, crude attempts at raising them have so far been unsuccessful.

In summary, crypsis in *Oliva* species is still far from being understood, but whatever its interpretation, the phenomenon is the rule rather than the exception in Hansa Bay.

4.2. Taxonomic consequences.

The colour pattern of *Oliva* shells is a character that has been of paramount taxonomic importance and still constitutes a large part of contemporary species descriptions. Our observations call for some comments on the use (and possible abuse) of this character, as many authors working on the genus *Oliva* seem completely unaware of the vast literature available on shell colour variation.

In Hansa Bay, most species of *Oliva* are cryptic and many are eurytopic. On the one hand, within the same eurytopic species, specimens imitating very dissimilar habitats will acquire greatly different aspects. On the other hand, syntopic populations of different species will mimic the same substrate and will thus tend to resemble each other (see Plate 1), forming local assemblages at first sight reminiscent of Müllerian groups of mimics (but this concept should be restricted to aposematic and not to cryptic colorations). So crypsis has two consequences: divergence within eurytopic species and convergence between syntopic species. This can obviously cause much taxonomic confusion and crypsis is thus likely

to have been a major contributor to the old "*Oliva* problem".

The taxonomic value of gross colour features should be considered with great caution. In Hansa Bay, the overall colour pattern of an *Oliva* specimen (especially with depth correction for colours) often gives more information on the underwater aspect of its habitat than it does on its taxonomic status. This remark does not apply to features of the ventral face (not seen by the predator) or to small details (the patterns of the spire, the fasciolar band, the subsutural zone, etc.) that hardly affect concealment. Such features, being less adaptive, are more likely to constitute reliable identification characters.

We see no reason why this situation should be restricted to the genus *Oliva* and one can expect crypsis to occur in other controversial groups of molluscs, with similar taxonomic consequences.

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Station (diving)	Map coord.	Depth (m)	Station (diving)	Map coord.	Depth (m)	Station (diving)	Map coord.	Depth (m)
A1	H5/b	0.7	**A25**	Z7/b	0.5	**A49**	X4/d	45
A2	J4/b	3	**A26**	J8/c	30	**A50**	Y2/b	15
A3	J4/b	2.5	**A27**	J7/d	17	**A51**	U2/a	15
A4	J4/b	4	**A28**	J4/d	3	**A52**	U2/a	15
A5	J4/b	6.5	**A29**	U2/c	18	**A53**	U2/a	15
A6	J4/b	6.5	**A30**	H7/d	17	**A54**	B7/b	40
A7	J4/b	4.5	**A31**	V2/b	31	**A55**	U2/a	15
A8	J4/b	2.5	**A32**	E3/a	25	**A56**	U1/b	10
A9	U1/b	0	**A33**	Z4/a	11	**A57**	Z9/c	0.5
A10	T2/c	10	**A34**	Z4/a	8	**A58**	U1/b	10
A11	K3/a	16	**A35**	Z7/b	6	**A59**	U1/b	0.5
A12	Z7/b	9	**A36**	W2/c	9	**A61**	Y7/d	22
A13	Z7/b	8	**A37**	W1/d	5	**A62**	Y7/d	17
A14	Z7/b	5	**A38**	U5/c	30	**A63**	J4/d	1
A15	F3/b	20	**A39**	V5/a	41	**A64**	J5/a	1
A16	S2/d	3	**A40**	T2/d	17	**A70**	U1/b	3
A17	N3/d	25	**A41**	J6/c	0.5	**A71**	V1/b	10
A18	N4/a	12	**A42**	U1/b	6	**A72**	S3/d	0
A19	H5/d	0.5	**A43**	Z9/d	10	**A75**	L8/c	30
A20	T2/a-c	4	**A44**	Y8/c	9	**A76**	H5/c	0
A21	T1/d	4.5	**A45**	Z6/b	4	**A77**	H5/c	0
A22	V1/b	7	**A46**	Z5/b	7	**A78**	H5/c	0
A23	T1/b	0.5	**A47**	S3/d	3	**A79**	V1/a	0
A24	Z5/b	0.5	**A48**	Y4/abcd	21	**S1**	W4/a	40

Station (Dredging)	Map coord.	Depth (m)	Station (Dredging)	Map coord.	Depth (m)
D1	Z7	6	**D13**	V1	5
D2	Z4	5	**D14**	W1	5
D3	U1	3	**D15**	W1	3
D4	T1	3	**D16**	W2	3
D5	T1	3	**D17**	V1	10
D6	U1	3	**D18**	W2	10
D7	U1	5	**D19**	W2	10
D8	U1	10	**D20**	U1	10
D9	U2	15	**D21**	U1	3
D10	Y2	10	**D23**	U1	5
D11	Y2	5	**D24**	U1	15
D12	V1	3	**A69**	Z9	10

Table 1. Identification of sampling stations. Coordinates refer to maps figures 1 and 2, where each surface unit was subdivided into *a* (upper left), *b* (upper right), *c* (lower left) and *d* (lower right).

Station	Granulometry (µm)							Carbon analysis		Substrate group
	>2000	2000> >1000	1000> >500	500> >250	250> >125	125> >63	<63	Org. C	CaCO3	
	%	%	%	%	%	%	%	%	%	
A.1	9.02	13.63	46.60	26.19	4.23	0.33	0.01	0.11	86.07	White
A.2	10.69	31.28	38.47	10.50	6.16	2.05	0.85	0.17	90.93	White
A.3	12.60	42.50	38.42	3.02	1.60	1.25	0.62	0.12	87.46	White
A.4	2.87	14.94	28.09	25.85	16.33	9.39	2.53	0.27	83.50	White
A.5	1.57	12.36	27.25	24.76	21.90	9.29	2.86	0.26	82.96	White
A.6	8.13	13.33	21.65	23.71	23.58	6.36	3.24	0.23	88.56	White
A.8	22.95	25.98	25.31	14.30	8.98	1.85	0.63	0.14	91.03	White
A.9	0.00	0.00	0.17	4.57	56.04	38.67	0.55	0.09	1.05	Black
A10	0.08	0.37	0.82	0.79	6.71	86.96	4.25	0.21	0.33	Black
A11	1.21	4.67	24.70	31.07	25.27	10.89	2.21	0.15	88.13	White
A12	0.03	0.08	1.56	7.62	60.70	29.03	0.98	0.16	82.40	White
A13	0.13	0.24	1.64	5.91	60.72	30.39	0.97	0.16	91.04	White
A14	0.00	0.13	2.76	28.09	65.54	3.42	0.05	0.12	93.18	White
A15	0.19	0.86	5.76	8.74	28.82	34.04	21.59	0.41	82.17	White
A16	0.07	0.31	1.42	12.10	64.11	21.64	0.34	0.10	0.01	Black
A17	1.05	1.21	6.78	13.35	39.84	28.43	9.35	0.24	84.70	White
A18	0.20	3.64	13.55	20.19	41.80	18.62	1.99	0.13	86.67	White
A20	0.05	0.11	0.76	6.45	53.00	38.96	0.66	0.11	0.00	Black
A21	0.20	0.44	0.92	3.12	49.33	44.01	1.99	0.12	0.89	Black
A22	0.03	0.33	1.00	4.40	21.77	64.36	8.11	0.27	1.54	Black
A23	0.03	0.25	1.14	6.90	51.38	39.49	0.81	0.01	1.70	Black
A24	1.35	0.19	0.54	0.98	34.91	61.23	0.80	0.02	2.90	Black
A25	0.47	0.97	5.04	29.37	63.31	0.85	0.00	0.11	92.93	White
A26	4.75	6.93	14.82	12.10	27.61	28.06	5.74	0.25	56.25	White
A27	16.96	15.65	23.24	15.70	17.38	8.88	2.19	0.29	87.79	White
A28	42.94	36.08	18.66	1.12	0.41	0.48	0.31	0.16	96.04	White
A29	0.05	0.45	2.82	3.37	9.52	59.06	24.73	0.29	5.68	Black
A30	9.23	10.19	16.94	16.21	30.72	14.44	2.26	0.28	87.13	White
A31	0.03	0.89	7.80	11.18	24.93	45.20	9.98	0.10	14.28	Black
A32	14.49	15.09	21.84	15.84	19.91	10.56	2.27	0.16	80.30	White
A33	0.51	0.45	1.35	2.76	40.17	51.16	3.59	0.08	3.52	Black
A34	0.65	0.12	0.61	0.95	14.25	74.04	9.37	0.14	3.42	Black
A35	.0.17	0.32	10.31	52.71	35.20	1.29	0.00	0.16	91.40	White
A36	1.22	0.28	0.56	2.85	22.80	65.57	6.72	0.27	3.03	Black
A37	0.20	0.31	1.03	2.17	26.33	64.49	5.48	0.36	1.53	Black
A38	14.65	12.05	20.10	20.28	25.37	6.16	1.38	0.27	86.96	White
A39	16.80	16.85	22.85	20.09	20.37	2.47	0.58	0.07	84.62	White
A40	0.30	0.67	2.33	1.86	10.17	76.16	8.51	0.19	2.73	Black
A41	23.90	8.77	10.92	11.72	38.94	5.73	0.01	0.20	91.53	White
A43	0.03	3.29	19.07	25.45	37.22	12.94	2.00	0.22	92.35	White
A44	2.52	2.02	2.62	70.82	21.22	0.80	0.00	0.22	89.56	White
A45	0.00	0.02	0.07	0.18	4.36	87.43	7.94	0.07	4.13	Black
A46	0.09	0.15	0.76	2.54	7.75	57.03	31.67	0.09	1.67	Black
A47	0.09	0.08	0.34	3.41	55.83	38.83	1.41	0.15	0.81	Black
A48	0.02	0.08	0.20	0.43	19.12	31.90	48.26	1.77	5.68	Black
A49	0.31	1.28	4.42	7.64	29.58	32.50	24.27	0.31	25.15	Black
A50	0.00	0.04	0.09	0.41	43.10	52.28	4.08	0.14	1.09	Black
A55	0.18	0.26	1.87	3.15	23.38	55.10	16.07	0.17	4.72	Black
A57	0.25	0.68	5.38	15.34	53.02	24.95	0.38	0.17	89.29	White
A58	0.00	0.12	1.35	3.35	35.08	52.70	7.40	0.11	0.94	Black
A61	0.00	0.04	0.28	4.91	17.42	48.10	29.26	0.43	37.67	Black
A62	0.00	0.02	0.43	1.61	23.23	48.26	26.45	0.35	58.19	Black
A63	28.99	24.27	41.90	2.63	1.50	0.67	0.04	0.14	86.28	White
A64	28.07	19.68	47.63	2.68	1.16	0.68	0.10	0.18	83.00	White
A70	0.31	0.16	0.31	1.83	39.00	55.78	2.60	0.06	0.87	Black
A71	0.00	0.11	0.36	0.38	3.76	68.91	26.47	0.55	2.85	Black
A72	0.00	0.02	0.14	0.48	50.31	49.02	0.03	0.06	0.66	Black
A75	22.26	17.30	28.74	19.43	10.28	1.79	0.20	0.19	91.86	White
A76	49.87	20.94	20.11	3.76	3.56	1.69	0.05	0.17	81.93	White
A77	37.07	7.10	7.98	5.82	25.94	16.08	0.00	0.16	91.91	White
A78	29.60	13.84	22.11	17.48	13.32	3.64	0.01	0.15	93.06	White
D12	0.02	0.38	0.98	15.45	61.05	21.22	0.89	0.12	0.58	Black
D13	0.05	0.12	0.75	23.38	69.21	5.96	0.54	0.14	1.25	Black
S1	0.11	0.31	1.97	3.27	17.45	28.62	48.28	0.56	42.31	Black

Table 2. Characteristics of sediment samples.

SPECIES	HABITAT	EXAMPLES
amethystina	coral sand near living coral, mostly 1-10m. Also around wrecks	A2, A3, A4, A8, A28, A30, A60
athenia	"black" sediment, 5-10m.	D13, D14.
buelowi	coral sand, bottom of reefs, 20-50m.	A32
bulbiformis	"white" or "black" sediment, 1-8m (shallow only in quiet waters).	A14, A24, A35, A42, D3.
carneola	"black" or "white" sediment, 0.5-30m (not in very agitated shallow waters).	A2 to A8, A10, A15 to A19, A21, A22, A 26 to A28, A36, A40, A42 to A45, A47, A51 to A53, A55 to A58, A60, A63, A64, A70, D7 to D9, D14, D16, D20.
ceramensis	"black" sediment, 10-31 m (generally 18-25m).	A10, A29, A31, A40, A51 to A53, A55, A56, A58, A61, D8 to D10, D19, D20, D24.
caerulea	coral sand, 0.5-3 m in Laing I. lagoon, 6m on Durangit Reef.	A1, A19, A63, A64, A76, A77, A78
concavospira	"black" sediment, 8-22 m (generally 12-18m)	A34, A50, A51. A52. A53. A55. A56. A58, A62
concinna	"white" sediment, 5-10 m (off Boro Beach only).	A14, A35.
DHB	"black" sediment, 3-12 m.	A13, A16, A20, A33, A45, A56, A58, A70, D12 to D15, D21, D23
dubia	very fine "black" sediment, 40-60 m.	
elegans	"black" sediment, 0.5-7 m near Sakula and Awar Rivers; "white" sediment (0.5-1 m) at Mandi Beach	A57, D15.
funebralis	"black" sediment; 3-7 m.	A70
longispira	"black" or "white" sediment, surf-exposed beaches only	A9, A23, A24, A25, A59, A79
mantichora	coral sand near living coral, mostly 20-40 m	A54
miniacea	coral sand, 10-18 m. Rare in Hansa Bay	A43
mucronata	"black" sediment, 5-8 m, mostly near Sakula River	A45
panniculata	coral sand, 6-20 m, agitated water (top of Durangit Reef).	A44.
parkinsoni	coral sand near reef, 12-42 m.	A11, A26, A27, A30, A32, A38, A39, A54, A75.
paxillus	coral sand, 6 m, agitated water.	top of Durangit Reef.
reticulata	"black" or "white" sediment, 0.5-12 m.	A13, A19, A37, A41, A44, A45, A57, A63, A64, A76, A77, A78, D1.
rufula	"black" sediment, 18-35 m (mostly 25-35m).	A29, A31.
sericea	coral sand, mostly 1-10 m. Also around wrecks.	A35, A63, A64
semmelincki	coral sand, bottom of reefs, 35-70 m.	A39
smithi	"black" or "white" sediment, 0.5-12 m.	A1, A12, A13, A14, A35, A45, A46, A57, A70, D1 to D6, D11, D12, D15, D21.
solomonensis	"black" or "white" sediment, 5-10 m.	A14, A35, A43, D13, D14.
tesselata	coral sand near reef, 3-7 m, only in lagoon.	A5.
vidua	"black" or "white" sediment, 0.5-12 m.	A1, A12, A13, A34, A45, A70, D3, D13, D14, D16, D17, D18, D20.
cfr. *volvaroides*	"black" or "white" sediment, 6 m. Very rare in Hansa Bay.	A22, A35.
ZHB	only found at one locality, 6 m.	Awar wreck.

Table 3. Brief notes on habitat of *Oliva* species, with collecting stations in February-March 1992.

Plate 1. (opposite)

1. *Oliva bulbiformis*. Laing Island lagoon. 1 m, "white" substrate.
2. *Oliva. solomonensis*. Off Boro Beach. 5 m, "white" substrate.
3. *Oliva caerulea*. Laing Island lagoon. 0.5 m, "white" substrate.
4. *Oliva concinna*. Off Boro Beach. 6 m, "white" substrate.
5. *Oliva elegans*. Mandi Beach. 0.5 m, "white" substrate.
6. *Oliva reticulata*. Laing Island lagoon. 1 m, "white" substrate.
7. *Oliva. reticulata*. Off Sisimangum. 5 m, "black" substrate.
8. *Oliva vidua*. NE of mouth of Sakula River. 5-7 m, "black" substrate.
9. *Oliva* sp. *DHB* (see text, section 2.1). NE of mouth of Sakula River. 5-7 m, "black" substrate.
10. *Oliva athenia*. NE of mouth of Sakula River. 5-7 m. "black" substrate.
11. *Oliva elegans*. NE of mouth of Sakula River. 5-7 m, "black" substrate.
12. *Oliva reticulata*. NE of mouth of Sakula River. 5-7 m, "black" substrate.


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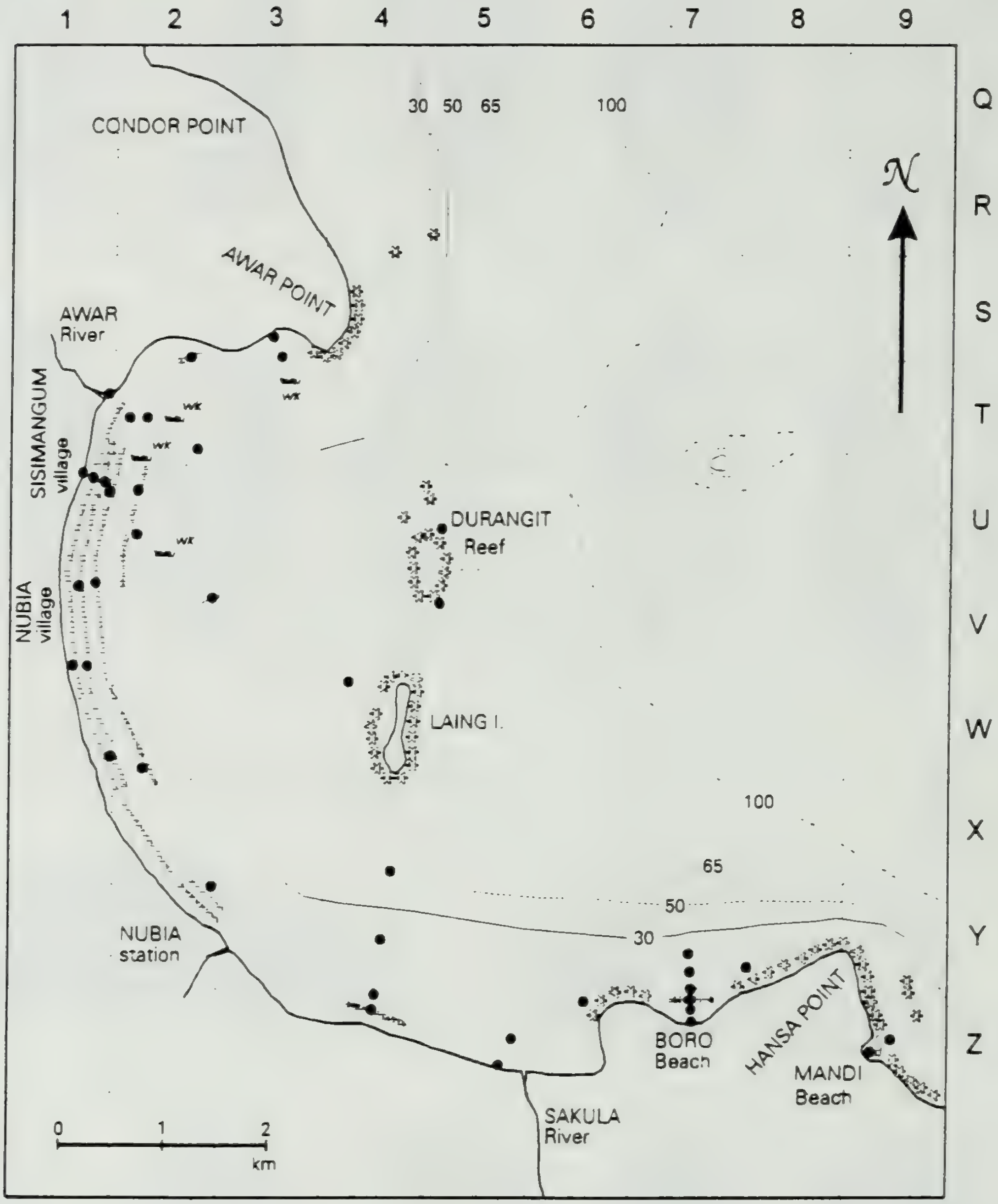

Fig. 1. Hansa Bay. Black circles represent locations of sediment samplings at sites where *Oliva* species have been collected during February-March 1992. Dredgings are represented by thick gray lines. Stars represent coral reefs.

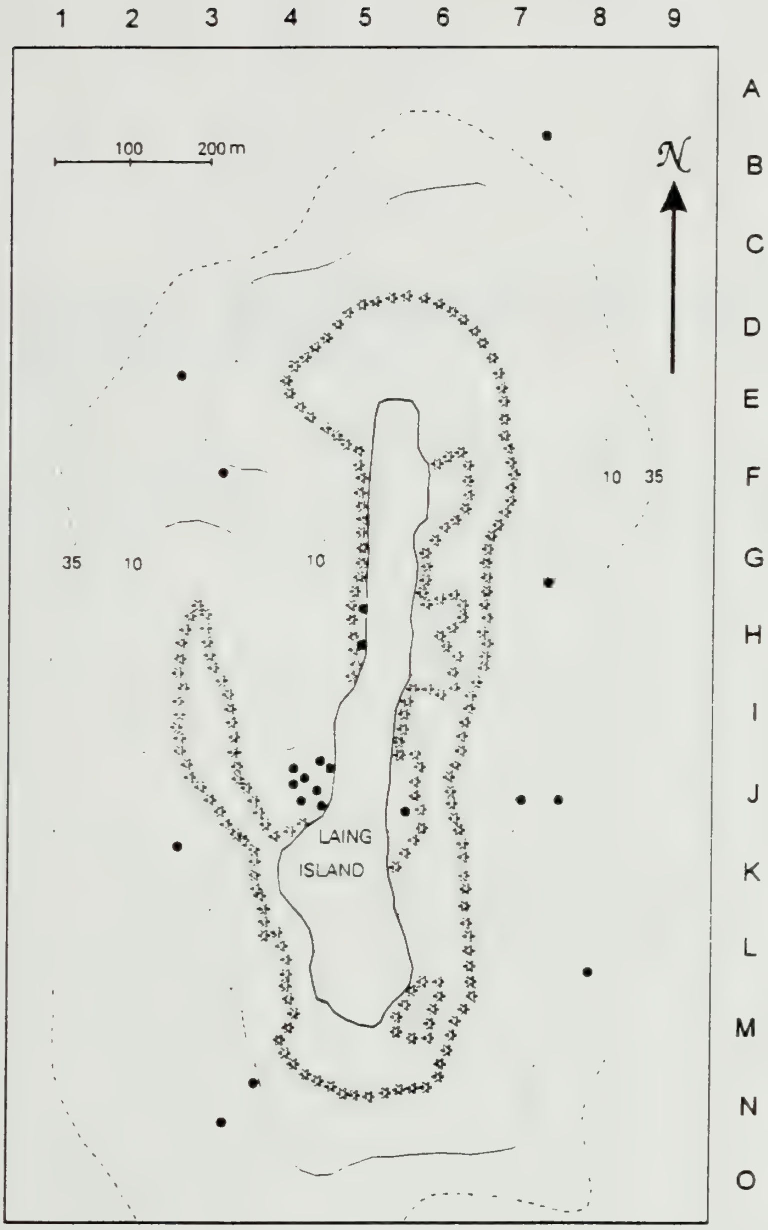

Fig. 2. Laing Island. Black circles represent locations of sediment samplings at sites where *Oliva* species have been collected during February-March 1992. Stars represent the limit of coral reefs emerging at low tide.

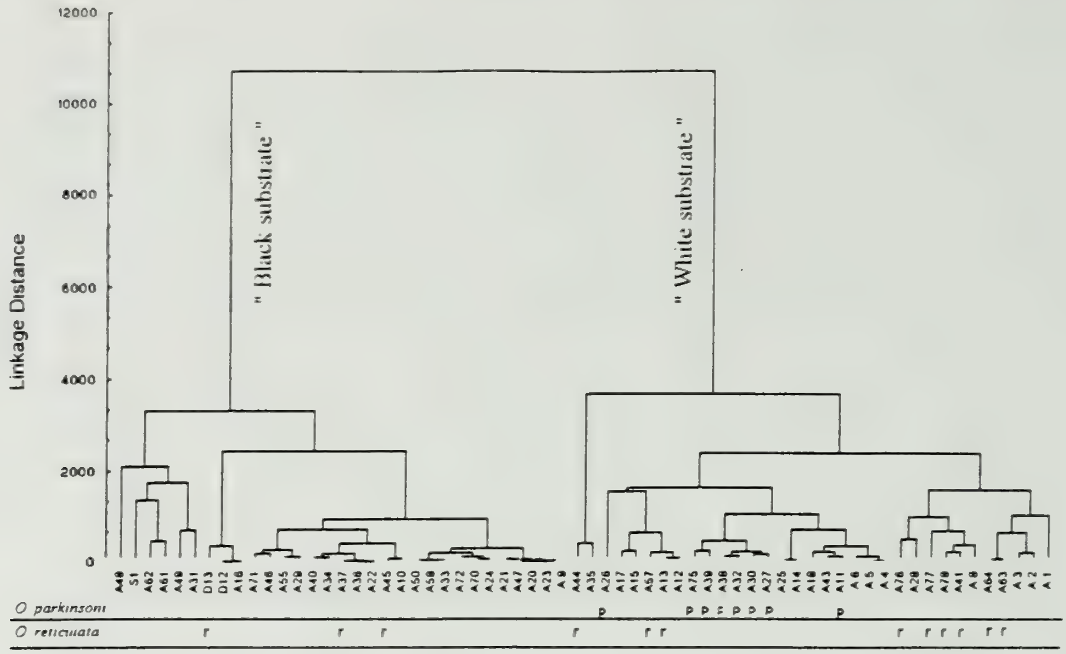

Fig. 3. U.P.G.M.A clustering (squared euclidian distances) of sediment samples. Variables: six textural classes (>2000 µm, 2000-1000 µm, 1000-500 µm, 500-250 µm, 125-63 µm and < 63 µm), percentage of organic carbon, percentage of carbonates and depth. The disjunct distributions of *Oliva reticulata* (r) and *O. parkinsoni* (p) are shown below the dendrogram, as an example.

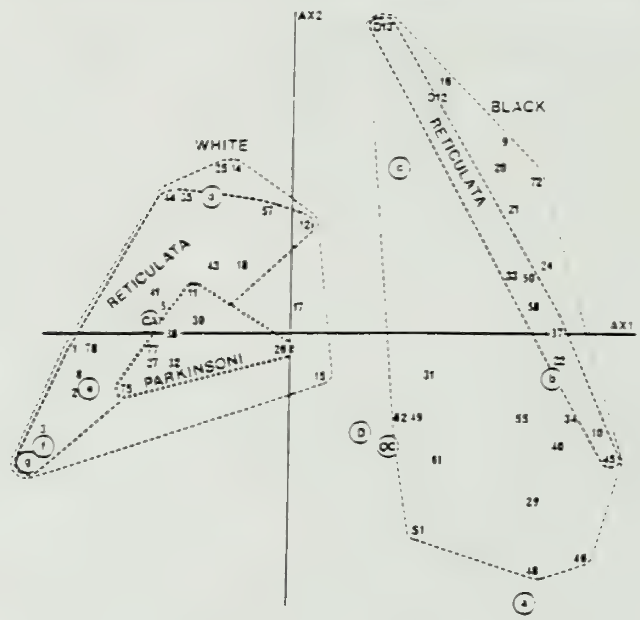

Fig. 4. F.A.C. (Factorial Analysis of Correspondences) analysis of sediment samples. Variables: seven textural classes [>2000 µm (g), 2000-1000 µm (f), 1000-500 µm (e), 500-250 µm (d), 250-125 µm (c) 125-63 µm (b) and < 63 µm (a)], percentage of organic carbon (OC), percentage of carbonates (CA) and depth (D). The disjunct distributions of *Oliva reticulata* and *O. parkinsoni* are shown as an example.

point seen	*point hidden*	*point seen*	*point hidden*	*point seen*	*point hidden*
CA	4	g	28	3	63, 64
5	6	22	36	24	70
12	13	32	39	46	71
20	23	20	47	f	76

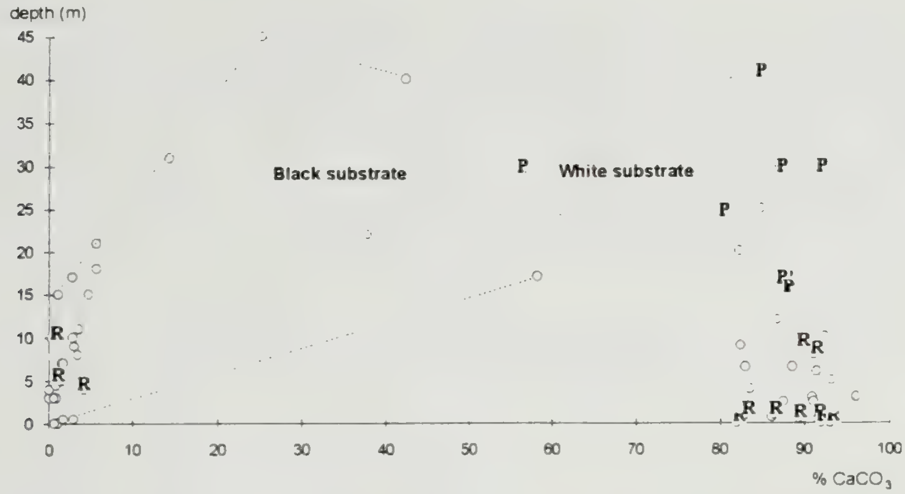

Fig. 5. Scatter diagram of % carbonates vs. depth. The two groups of sediments are again separated on this simplified representation. The disjunct distributions of *Oliva reticulata* (R) and *O. parkinsoni* (P) are shown as an example.

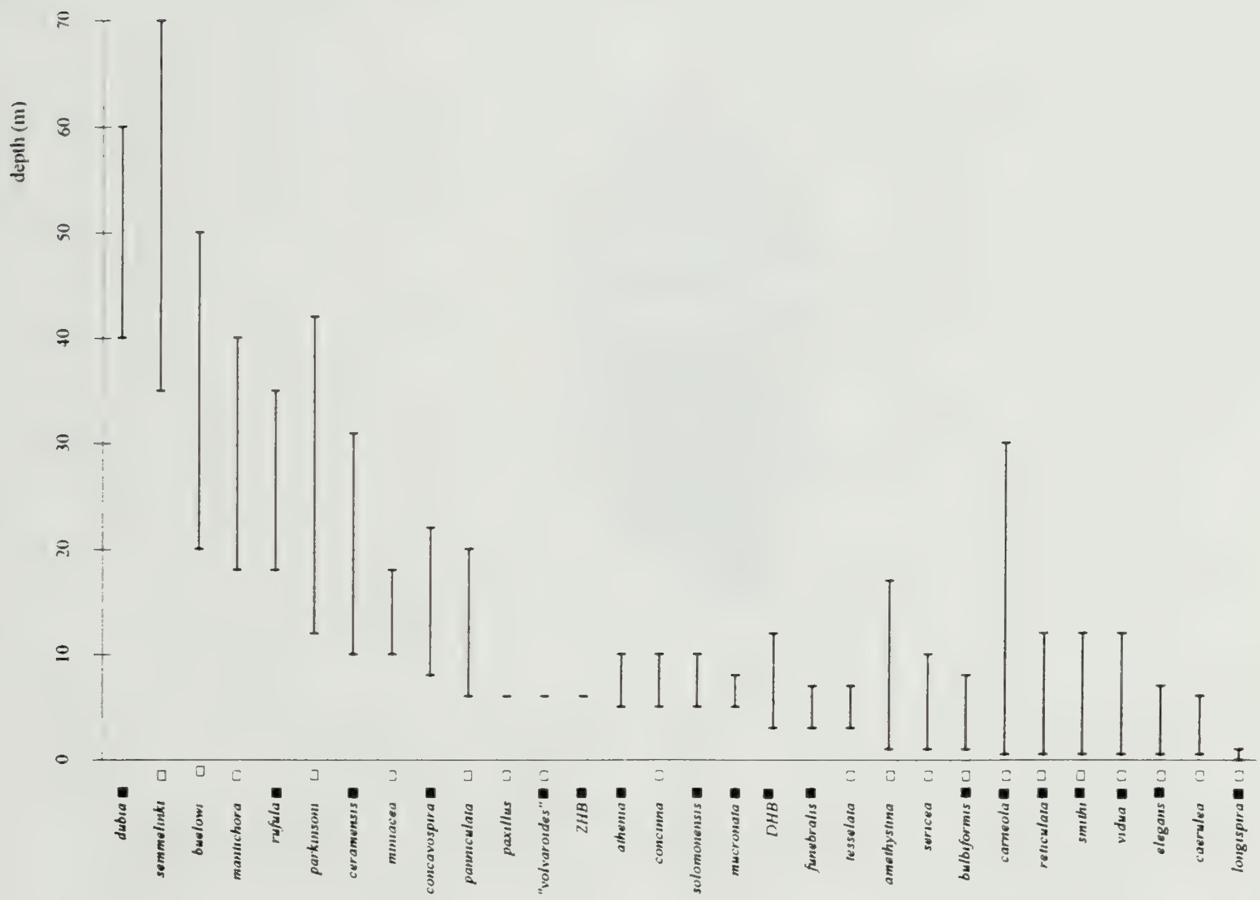

Fig. 6. Observed bathymetric range of *Oliva* species in Hansa Bay. Data from 1974 to 1993 (see text section 3.2.1). Black and white squares indicate occurence in "black" and "white" sediments, respectively.

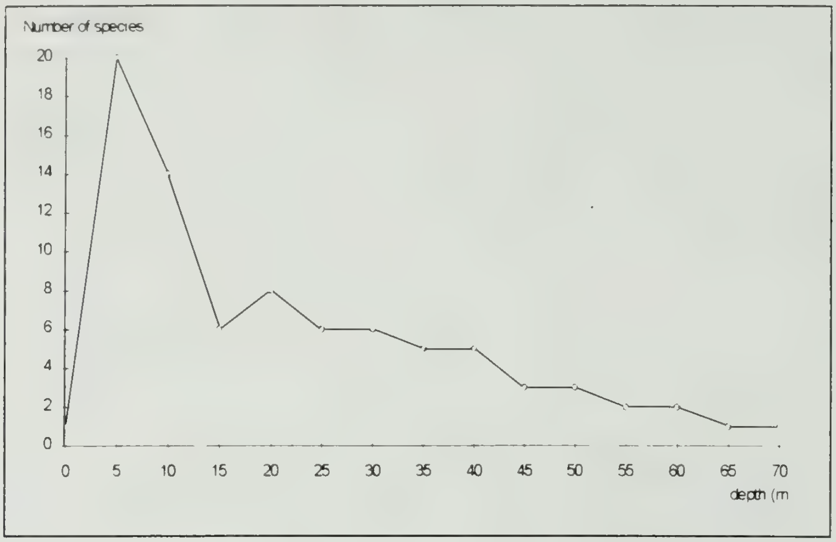

Fig. 7. Number of *Oliva* species in Hansa Bay as a function of depth.

Fig. 8. Aposematic pattern of the toxic species *Oliva rufula* (trapped NW of Laing I., 35 m, "black" substrate). Scale bar: 10 mm.

Studies on Olividae. XIX. Where is the suture of *Oliva* shells?

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ABSTRACT. The suture of *Oliva* shells is hardly perceptible and has no functional link with the so-called "sutural channel", for which the more descriptive name "filament channel" is proposed.

RESUME. La suture des coquilles d' *Oliva* est à peine perceptible et n' a pas d'association fonctionnelle avec le soi-disant "canal sutural", pour lequel le nom plus descriptif de "canal du filament" est proposé.

KEYWORDS: *Oliva*, shell, suture, channel, posterior filament, filament channel.

1. INTRODUCTION.

All authors agree broadly on the definition of the suture of coiled shells. This is for instance: "*the line of contact where two whorls meet*" (FRETTER & GRAHAM, 1962), or "*a continuous line marking the junction of whorls in a gastropod shell*" (ARNOLD, 1965), or "*the junction of each whorl against the other*" (ABBOTT, 1974).

The spire of all *Oliva* shells displays a wide, conspicuous spiral channel that LAMARCK (1811) called "*le canal de la spire*". In their descriptions of the general characters of the genus *Oliva*, FISCHER von WALDHEIM (1807), MONFORT (1808), LAMARCK (1811) and later DUCLOS (1844) all repeated *verbatim* the same expression: "*tours de spire séparés par un canal*".

If the whorls were "separated by a channel", then it was quite logical to associate the channel with the suture and DUCLOS (1844) indifferently used "*canal*", "*canal spiral*" and "*canal sutural*". From there on, the habit was established and until today nobody questioned the appropriateness of the channel-suture association. For instance, one finds the terms: "*groove on the suture*" in GRAY (1842), "*sutural canal*" in MARRAT (1871) and PETUCH & SARGENT (1986); "*sutural channel*" in TURSCH & GERMAIN (1985); "*suture canaliculated*" in TRYON (1883); "*channeled suture*" in ZEIGLER & PORRECA (1969), ABBOTT (1974) and KANTOR (1991); "*suture*" in KANTOR (1991), TURSCH & VAN OSSELAER (1987), VAN OSSELAER & TURSCH (1988); "*open suture*" in GREIFENEDER (1981).

Amongst gastropods, the "channeled suture" is found only in the family Olividae where it is a hallmark of the genera *Oliva*, *Olivella*, *Olivancillaria* and *Agaronia*. It has been shown to constitute an operational taxonomic character in the genus *Oliva* by TURSCH & GERMAIN (1985), TURSCH & VAN OSSELAER (1987) and VAN OSSELAER & TURSCH (1988). The "channeled suture" seems to be a very important feature, as it is always maintained open (at least on nearly one full volution) even in the many species where the spire is covered with a thick callous layer. The channel is also present in freak specimens. It is a very old feature, clearly displayed in the oldest *Oliva* shells (such as the Miocene fossil *O. dufresnei* Basterot, 1925). The "channel" appears right after the protoconch transition and is already present in very juvenile specimens.

One would predict that a structure so carefully preserved both in phylogeny and in ontogeny has to be functional, but what could that function be? From early days, the channel was related to a peculiar organ, the *posterior filament*. The first observation we could trace was in QUOY & GAIMARD (1834): "*le manteau ... se termine en arrière par un filament plus ou moins long qui se loge dans le canal tout particulier que forment les sutures de la spire*". GRAY (1842) writes of "*the thread-like elongation at the hinder angle, which forms the groove on the suture*". TRYON (1883), in the general characters of the subfamily Olivinae,

writes: "*an appendage behind which reposes in the channeled suture*". In OLSSON (1956), one finds: "*In Oliva, the channel in the suture is maintained open and deep by a slender, tail-like appendage attached to the back of the mantle. This appendage lies along the channel when the animal is expanded but is lifted out as the soft parts are pulled back in the shell. Its real purpose is unknown*". KEEN (1971) writes: "*The mantle edge also has an unusual threadlike extension that lies along the suture, called a filament, which probably has a sensory function*".

2. OBSERVATIONS

2.1. Observations of shell sections.

Examination of polished longitudinal sections of the shell of several *Oliva* species brought unexpected results. Figure 1 shows the part of the shell that will be examined here.

The two external crystal layers of each whorl are very easily recognised and allow easy localizing of the external boundary of each whorl. In all the sections (figures 2, 3 and 4) one can see in each whorl that the channel (c) lies in the third, cross-lamellar layer, counting from outside.

On the sections of *Oliva reticularis* Lamarck, 1811 (Fig. 2) and of *O. reticulata* (Röding, 1798) (Fig. 3) the suture (s) is clearly separated and well above the channel (c). For the latter, one should note that the suture now lies close to a channel, but it is the channel of the *preceding whorl* ! This is the most usual case amongst *Oliva*. Albeit easily detectable on polished cuts, the real sutural line of these *Oliva* is nearly invisible on the intact shell, even under magnification. The location of the suture cannot be guessed at by changes of coloration on the whorls of the spire: these are generally due to variations in the thickness of the outer layer.

An interesting and common case is that of some heavily calloused shells, such as the specimen of *Oliva carneola* (Gmelin, 1791) illustrated in Figure 4. The channel is still distinct from the external boundary of the preceding whorl, as in the previous examples. But in this shell, every volution entirely covers the whole spire and there is no external line marking the separation between consecutive whorls. In such cases the common concept of suture (as *a continuous line marking the junction of whorls*) does not make sense.

2.2. Observations on live specimens

The posterior filament has been routinely observed for about thirty species of *Oliva* of which we have studied the live animal. For every species, the filament (when extended) could be seen lying inside and along the spiral channel, as schematically depicted in Figure 5. This fully confirms the relationship described by earlier authors. A clear sketch of the positioning of the posterior filament of *Olivella biplicata* has been published by BURCH (1988). One should note that the posterior filament is not always obvious because in many species it is nearly translucent.

3. DISCUSSION

Our observations show clearly that the spiral channel of *Oliva* shells is completely distinct from the suture. The real suture is never "*canaliculated*" or "*channeled*" and is hardly visible on the shell. The classical names "*sutural canal*", "*sutural channel*" or "*suture*" that have been applied to the channel are misleading and have to be replaced. Because of its obvious association with the posterior filament, we suggest that it be named the **"filament channel"**.

The shape of the transversal section of the filament channel differs from species to species and several examples have been illustrated in TURSCH & VAN OSSELAER (1987). These features can be utilised as operational taxonomic discriminants (see TURSCH & VAN OSSELAER, 1987 and VAN OSSELAER & TURSCH, 1988).

The function of the channel is most probably that of a protecting sheath for the posterior filament. The function of the posterior filament itself still remains a mystery, in spite of the anatomical study of MARCUS & MARCUS (1959). The possibility of the filament being a sensory organ was raised by KEEN (1971). BURCH (1988) reports that the posterior filament senses water currents. Several alternative hypotheses (among which the production of chemical messengers) could be considered. Work on this subject is being pursued in this laboratory for some years but no firm conclusion has been reached so far. The exact function of the filament is a fascinating problem but has no bearing on the conclusion reached here above, i.e. that the channel is not related to the suture.

This case is a fine demonstration of the necessity of checking old postulates. The assumption that the channel was related to the

suture was so logical that for nearly two centuries it was never questioned by any of the many students of *Oliva*. Ironically, this was also the case for the authors of this paper, who performed numerous, detailed measurements on a feature (the filament channel) that was erroneously called "the suture". The name of the character does of course not affect the taxonomic applications (TURSCH & GERMAIN, 1985; TURSCH & VAN OSSELAER, 1987; VAN OSSELAER & TURSCH, 1988) for which these measurements were proposed.

Acknowledgements.

We thank Mr. G. Bernardinis (Department of Geology) for his kind help in preparing the shell sections and Mrs. N. Van Mol (Department of Animal Biology) for the line drawings.

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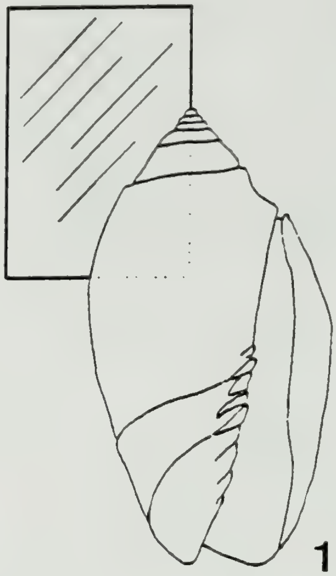

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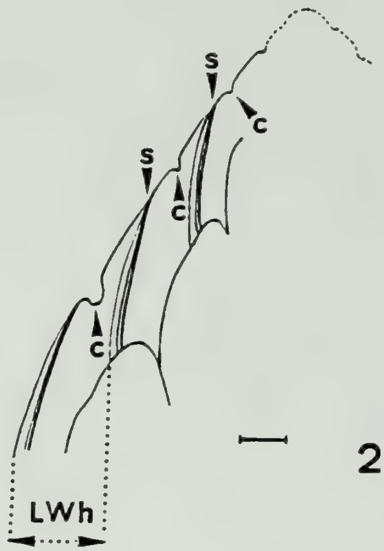

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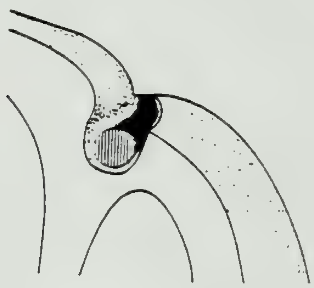

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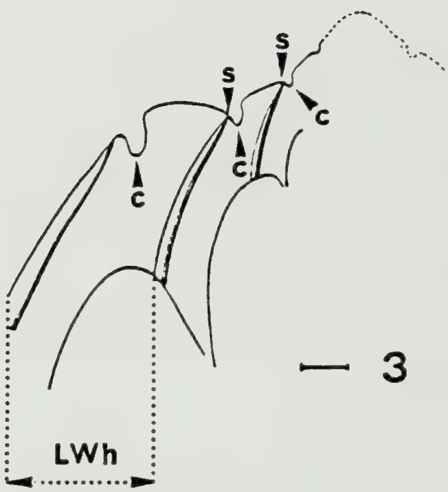

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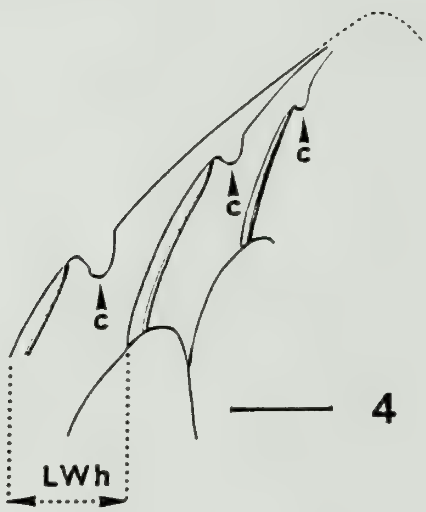

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Fig. 1. Plane of the observed cuts in *Oliva* shells.
Fig. 2. Section of *Oliva reticularis* Lamarck, 1811. **s**: suture. **c**: filament channel. **LWh**: last whorl. Scale bar: 1 mm.
Fig. 3. Section of *Oliva reticulata* (Röding, 1798). **s**: suture. **c**: filament channel. **LWh**: last whorl. Scale bar: 1 mm.
Fig. 4. Section of *Oliva carneola* (Gmelin, 1791). **s**: suture. **c**: filament channel. **LWh**: last whorl. Scale bar: 1 mm.
Fig. 5. Schematic view of a portion of the posterior filament lying in the filament channel. In reality, the filament (represented in black for the sake of clarity) is nearly translucent in many species. Its relative size has also been exagerated.

Studies on Olividae. XX. The pre-Lamarckian names for *Oliva* species

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ABSTRACT. The nomenclatural status of each of the *Oliva* names introduced by Linnaeus (1758), Born, (1778), Schröter (1782), Lightfoot (1786), Abel (1787), Karsten (1789), Gmelin (1791), Röding (1798), Link (1807), Fischer (1807), Montfort (1808) and Perry (1811) has been re-examined. Of the 88 names proposed by these authors 14 have been retained as valid *Oliva* names. We have been compelled to replace two well known names: *Oliva vidua* (Röding, 1789) by *O. nigrita* (Karsten, 1789) and *O. tessellata* Lamarck, 1811 by *O. olivacea* (Karsten, 1789).

RESUME. Le statut nomenclatural des noms d' *Oliva* introduits par Linné (1758), Born, (1778), Schröter (1782), Lightfoot (1786), Abel (1787), Karsten (1789), Gmelin (1791), Röding (1798), Link (1807), Fischer (1807), Montfort (1808) and Perry (1811) a été réexaminé. Des 88 noms proposés par ces auteurs, 14 ont été retenus comme noms valides pour des *Oliva*. Nous avons été forcés de remplacer deux noms bien connus: *Oliva vidua* (Röding, 1798) par *O. nigrita* (Karsten, 1789) et *O. tessellata* Lamarck, 1811 par *O. olivacea* (Karsten, 1789).

KEYWORDS : Mollusca, Gastropoda, Olividae, *Oliva*, nomenclature.

INTRODUCTION

Is a review of the old *Oliva* names still necessary? It is true that nearly all the names analysed here are well known to recent authors and can be found in the indexes of popular publications. The problem is that many of the attributions are uncritical citations, mainly from the pioneering works of BURCH & BURCH (1960, 1967). This can be demonstrated for instance by the ubiquitous use of *aurata* (Röding, 1798), a very obvious *nomen nudum*, to designate a variety of the species known as *Oliva vidua* (Röding, 1798). There is simply no way of guessing what *aurata* might be and it is obvious that the original description has not been checked. Divergent attributions are also frequent, as will be seen hereunder. Both factors are major causes of the well-known nomenclatural confusion in the genus *Oliva*. A critical, *de novo* analysis of all the original sources was thus deemed necessary. A chronological approach is clearly the simplest way of automatically detecting junior homonyms and synonyms. Some of the points discussed in this paper might appear to be insignificant details. For instance, is it really important to know if the name given to a "bad species" is a *nomen nudum* or a *nomen dubium*? The matter is actually of importance and does shape the subsequent nomenclature, because a *nomen nudum* remains available for future re-use.

The identification of the species described by the old masters is straightforward only when the type material has been preserved. For *Oliva*, this is the case only for LINNAEUS (studied by OLSSON & DANCE, 1966) and FISCHER von WALDHEIM (studied by IVANOV & KANTOR, 1991). For all the others, identification problems are the rule rather than the exception.

The descriptions of the pre-Lamarckian authors are frequently insufficient for positive identification. They are nearly always extremely short and often based upon characters (such as the colour pattern) that are known today to be highly variable in the genus *Oliva*. We doubt that even a single species could be unambiguously recognised by its description alone. Fortunately, the authors do mostly (but not constantly) refer to previously published illustrations, which then constitute "indications" in the sense of art. 12 b (7) of the Code. The principal sources of these illustrations (amounting to over 90% of the total) are ADANSON (1757), d'ARGENVILLE (1742), BONNANI (1681, 1709), GUALTIERI (1742), KLEIN (1753), KNORR (1760-73), LISTER (1682-1695), MARTINI (1769-1795), PETIVER (1767), RUMPHIUS (1705), SEBA (1734-65) and SCHRÖTER (1782, 1783). Some of these figures are of very high quality and can be interpreted without ambiguity. Many others (quite rightly qualified as "medieval cartoons" by irreverent young students) are entirely unidentifiable. In some cases one may even doubt that the figure depicts an actual specimen.

Problems of image identification are compounded by the fact that the concept of species of ancient authors was quite different from ours. This is evidenced by the very common use of conflicting illustrations in support of a given name and the use of the same illustration for different names by the same author. Let us cite BURCH & BURCH (1967): "*It is tragic that we are compelled to abandon such solid material* (note: this refers to names supported by type material) *and accept references to a series of poorly drawn old wood cuts. Typical of these are some of Röding in the notorious Museum Boltenianum in which for some, Röding lists as many as four references all to entirely different species, some of them unrecognizable, and the actual shell has been sold as a curio and lost. What the species may have been is known only to God*". The frequency of such contradictions would make sense only if the descriptive conventions of the 18th century were different from ours. It is our feeling that many of the ancient authors cited previous illustrations to report resemblance rather than conspecificity in its present meaning.

In such conditions, reconciling the ancient species concepts with the rigid rules of the modern Code of Zoological Nomenclature (hereunder referred to as "the Code") necessarily entails some interpretation of the message the old masters might have wanted to convey. In doing so, our main concern has been nomenclatural stability. Changes to the presently accepted names have been made only when this was inevitable.

This paper deals only with recent species. For each author, only new names have been considered, previously utilised names being without nomenclatural interest (they are necessarily junior homonyms), the only exception being a previous *nomen nudum* (which remains available). Names that are obviously incompatible with *Oliva* species have not been considered. For each name, the original description has been reproduced *verbatim* in order to allow a verification of our conclusions. The only modification brought to the original texts is that for each author, species have been presented in alphabetical order (in their original spelling), for the facility of the reader. Divergent attributions in recent works frequently consulted by *Oliva* students are given in notes.

1. The *Oliva* of Linnaeus, 1758.

The species of *Oliva* described by Linnaeus in the tenth edition of the *Systema Naturae* were originally placed in *VOLUTA, Cylindroidae f. subcylindricae*. In citations of these species, the name of Linnaeus should thus be enclosed in parentheses (Code, art. 51 c).

The *Oliva* of Linnaeus pose no more problem, having been studied by HANLEY (1855) and adequately revised by OLSSON & DANCE (1966), who carefully examined the type material at the Linnean Society, London. No specimen of *Oliva* has been reported in the Linnean collection at Upsala (HOLM, 1957).

ispidula (p.730, sp.351)

ORIGINAL DESCRIPTION:
Ispidula. 351. V.testa cylindroide laevi, spira prominente margine unico.

*Rumph.mus.*t.39.f.6,7.

*Pet.gaz.*t.59.f.8.

Habitat . .

DISCUSSION. This name, cited here only because it has brought so much confusion in the *Oliva* literature, has already been discussed in great detail by OLSSON & DANCE (1966). The selected lectotype is not an *Oliva* but a fossil *Agaronia* (*Agaronia plicaria* Lam., 1811).
STATUS: **not an *Oliva*.**
Note: the name *ispidula* has not been rejected as a secondary homonym and remains available for an *Oliva* species not described under *Voluta*.

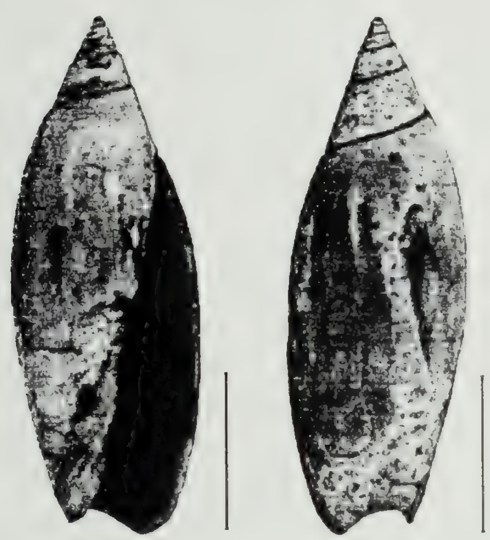

Fig. 1. "*Voluta*" *ispidula* L., 1758. Type specimen, Linnean Society of London. Scale bar: 1 cm.

oliva (p.729, sp.350)

ORIGINAL DESCRIPTION:
Oliva. 350. V.testa cylindroide laevi, spirae basi reflexa.

*List.Conch.*4.f.10.c.l.t.2.

*Rumph.mus.*t.39.f.2-5.

*Gualt.test.*t.23.f.B.

*Argenv.conch.*t.16.f.R. Litterata.

Kratzenst.Regenf. 2.t.1.f.2.

Habitat in M.Indico.

Varietates coloribus infinite ludentibus; Litterata praefertur.

DISCUSSION. This name has already been discussed by Olsson & Dance (1966), who selected and illustrated a lectotype, preserved at the Linnean Society, London. Linnaeus very fittingly called attention to the extreme variability of this species and the name should be used with caution. The lectotype seems to correspond to one of the species of the "*Oliva oliva* complex", the taxonomic structure of which has been discussed by TURSCH, MISSA & BOUILLON (1992).
STATUS: **valid name**.

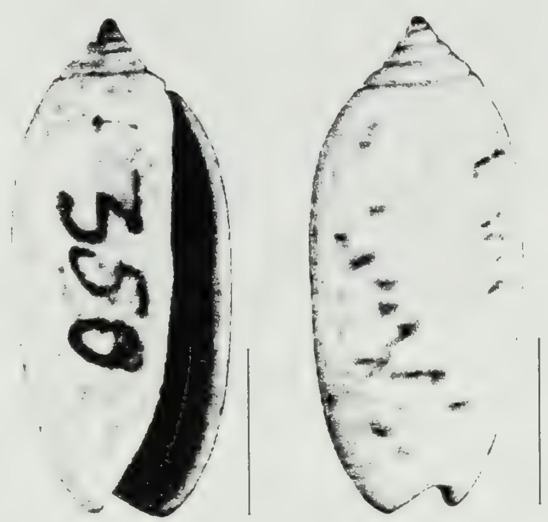

Fig. 2. *Oliva oliva* (L., 1758). Lectotype, Linnean Society of London. Scale bar: 1 cm.

porphyria (p.729, sp.349)

ORIGINAL DESCRIPTION:
porphyria 349. V.testa cylindroide laevi, spirae basi oblitterata, labro medio retuso.

*List.Conch.*t.727.

*Rumph.mus.*t.39.f.1.

*Gualt.test.*t.24.f.O.P.

*Argenv.conch.*t.16.f.K.

*Kratzenst.Regenf.*8.t.2.f.15.

Habitat . .

Affinitas tanta cum sequenti, ut potius varietas, quam distincta species, quamvis pretium eam nobilitaverit.

DISCUSSION: This name has already been discussed by OLSSON & DANCE (1966), who selected and illustrated a lectotype, preserved at the Linnean Society, London. The lectotype corresponds to the unanimous, traditional concept of this species.
STATUS: **valid name**.

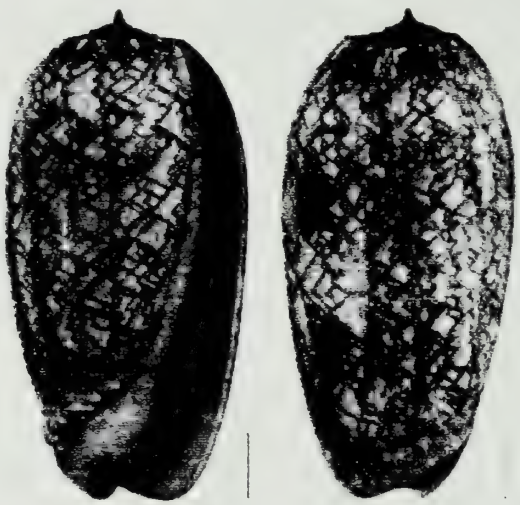

Fig. 3. *Oliva porphyria* (L., 1758). Lectotype, Linnean Society of London. Scale bar: 1 cm.

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2. The *Oliva* of Born, 1778, 1780.

No new olive name was given by Born, but one should consider his *ispidula*, which name being still available for an *Oliva* since *ispidula* (L, 1758) has been shown not to belong to this genus).

ORIGINAL DESCRIPTION:

In the *Index* (dating from 1778 according to RUTSCH, 1956), Born started his description:
F.II.4. Voluta ispidula. Die Spizdattel. Linn. S.N. Sp. 400
Testa subcylindrica laeui, spira conica, suturis acutis, columella incrassata oblique plicata. Die einigermassen walzenförmige glatte Schale hat einen glatten kegelförmigen scharfrandingen Schnirkel, und eine dichte schief gespaltene Spindel.

Born then listed a number of colour varieties (from α up to χ) over the next two pages, starting with:

α albida, brunno maculata. Weisslich, mit braunen Flecken.

In the *Testacea* (1780), one finds the same varieties, with the same reference figures and a description:

Testa emarginata subcylindrica, laevis; spira conica, longior; Anfractuum suturae acutae; Columella incrassata, oblique plicata. Dignoscitur a. V. Oliva, cui multum est affinis, basi spirali tumida, neque reflexa; Colorum differentia varietates, quas adduximus distinguit. Long 2 poll 9 lin. lat. 1. poll Patriam ubi constitit, varietatum descriptioni addidimus.

DISCUSSION. This case presents obvious contradictions and it deserves careful consideration, as identical situations will occur for the same species treated by subsequent authors. On the one hand, there is an explicit reference to "Linn. S.N. Sp. 400" (*ispidula* in the 12th edition of the *Systema Naturae*). On the other hand, the description of colour varieties and the large size "2 poll 9 lin".(about 74.6 mm) are quite incompatible with the fossil French *Agaronia* of Linnaeus.
The many illustrations supporting the descriptions of the numerous varieties are very conflicting. Bearing in mind that the concept of species at the time was quite different from ours, it is safer by far to conclude that the reference to "Linn. S.N. Sp. 400" indicates that Born referred to the species already described by Linnaeus.

Note: this species is *flammulata* Lamarck, 1811 according to BURCH & BURCH (1960).

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3. The *Oliva* of Schröter 1782, 1783.

No new olive name was given by Schröter, but (as in the case of Born) one should consider his *ispidula,* this name being still available for an *Oliva* since *ispidula* (L, 1758) has been shown not to belong to this genus).

The argument used in the case of Born also applies here and explicit references (both in the *Musei Gottwaldiana* and in the *Einleitung*) are taken to indicate that Schröter referred to the species already described by Linnaeus.

4. The *Oliva* of Lightfoot-Solander, 1786.

Lightfoot was the real author of the Portland Catalogue, as shown by DANCE (1962) and REHDER (1967) (see also IREDALE, 1916, DALL, 1921, KAY, 1965). Lightfoot utilised manuscript names given by Solander (his notes, formerly in the Banks collection, are now in the library of the British Museum, according to Rehder) and added a few names of his own invention.

Only one species of *Oliva* was published in the Portland Catalogue. It was described as *Voluta* and in citations of this species, the name of Lightfoot should thus be enclosed in parentheses (Code, art. 51 c).

One should note that Lightfoot did not describe species as such, but described lots of an auction. The same species can thus appear in two different lots. This is the case of:

incrassata (p. 13, # 264)

This shell appears in lots 264, 2315 and 3696.

ORIGINAL DESCRIPTION:

264. Voluta incrassata, S. Martyn, 499, 500 .... very rare.

2315. "A fine specimen of Voluta incrassa, S. Martyn, Vol. II - *very rare*, f. 499. 500."

3696. "*A very fine pair of Voluta Incrassata*, S. extremely scarce ...Martyn, vol. II. 499. 500."

DISCUSSION. Figures 499 and 500 of Martini (written "Martyn" by the author) clearly correspond to the unanimous present concept of this species.

STATUS: **valid name**.

Rehder draws attention to "*incrassa*", which he considers to be a misspelling of the trivial name. DILLWYN (1817) refers to other manuscript *Oliva* names of Solander. These are:

aurora MSS.
baltheata MSS.
cruenta MSS.
maculata MSS.
ventricosa MSS.

These names of Solander, being manuscript, have no nomenclatural standing. They are best referred to as (Solander) Dillwyn, 1817.

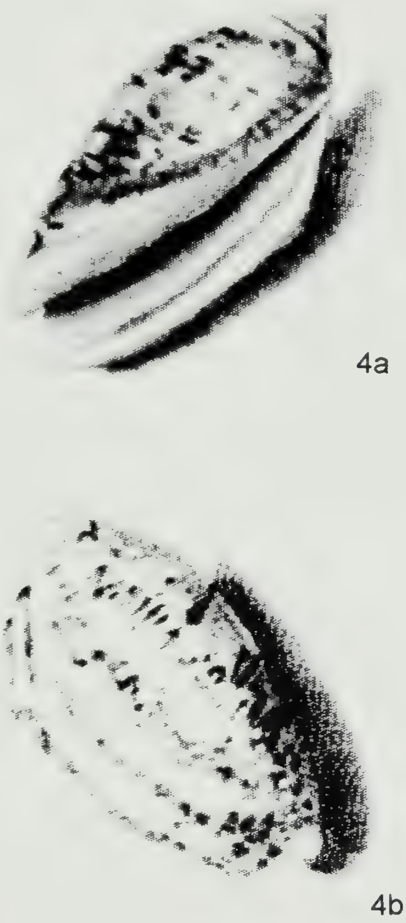

Fig. 4. *Oliva incrassata* (Lightfoot, 1786). 4a: Martini, fig. 499. 4b: Martini, fig. 500. Scale 1:1.

Notes:

- *aurora* (Solander) Dillwyn, 1817 is *carneola* (Gmelin, 1791) for BURCH & BURCH (1960), a color form of the same for PETUCH & SARGENT (1986).
- *baltheata* (Solander) Dillwyn, 1817 is *annulata* (Gmelin, 1791) for BURCH & BURCH (1960), WAGNER & ABBOTT (1978).
- *cruenta* (Solander) Dillwyn, 1817 is *annulata* (Gmelin, 1791) for BURCH & BURCH (1960), WAGNER & ABBOTT (1978).and ZEIGLER & PORRECA (1969) and *emicator* Meuschen (non binominal) for DAUTZENBERG (1927).
- *maculata* (Solander) Dillwyn, 1817 is *tigrina* Lamarck, 1811 for BURCH & BURCH (1960) and WAGNER & ABBOTT (1978).
- *ventricosa* (Solander) Dillwyn, 1817 is *bulbosa* (Röding, 1798) for BURCH & BURCH (1960), WAGNER & ABBOTT (1978) and PETUCH & SARGENT (1986).

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5. The *Oliva* of Abel, 1787.

Abel (1787) introduced new names such as *Voluta reticulata* and *Voluta porphyrea*. But there are good reasons to consider Abel as being not consistently binominal. In the *Voluta* section alone, one species has two names (p.66, n°1: *Voluta oliva - Vidua mauritana*). Others like *sepultura principis* (p; 67, n°9) and *vellus aureum* (p. 68, n° 13) bear no generic name. Many species were referred to only by a vernacular name, for instance "*Die grosse Panamarolle*" (p. 69, n° 21). In our opinion, these facts constitute sufficient grounds for rejecting all the names of Abel.

---

6. The *Oliva* of Karsten, 1789.

In the *Museum Leskeanum* - a work that appears to be consistently binominal (DUCHAMPS & TURSCH, 1994)- Karsten introduced two new names (*olivacea* and *nigrita*) on p. 216. Both names bear explicit reference to Martini but the work of that author has been officially rejected as non-binominal. Under the provisions of the Code, his names remain available and have to be considered here. The *Oliva* of Karsten were described as *Voluta* and in citations of these species, the name of the author should thus be enclosed in parentheses (Code, art. 51 c).

olivacea (p.216, # 638)

ORIGINAL DESCRIPTION:

Voluta olivacea Mart.

638 V. oliv. testa albida, punctis ex violaceo lutescentibus maculata, apertura atque columella omnino amethystinis.

Martini Konch. Kab. T.2.tab. 46. fig. 493. 94.

Long. 10 lin. lat 5 lin..

DISCUSSION: The original description and the colour figures of Martini undoubtedly represent the very characteristic shell now known as *tessellata* Lamarck. The figures were indeed cited by Lamarck himself for *tessellata*. The measurements given by Karsten (a precursor of biometry) indicate the shell is twice as high as wide. We have verified that this is nearly exactly the case for *tesselata*. With much reluctance we are compelled to conclude that *olivacea* Karsten is the earliest name for the well-known *tessellata* Lamarck (the type material of which has disappeared), which becomes an objective junior synonym as Lamarck referred to the same figures as Karsten.

STATUS: **valid name**.

5a 5b

Fig. 5. *Oliva olivacea* (Karsten, 1789). 5a: Martini, fig. 493. 5b: Martini, fig. 494. Scale 1:1.

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nigrita (p. 216, # 639, 640, 641)

Under the name *nigrita* Karsten grouped his sections 639, 640 and 641. The note under 641 clearly indicates that the author considerred these as varieties or forms of the same species.


6a


6b

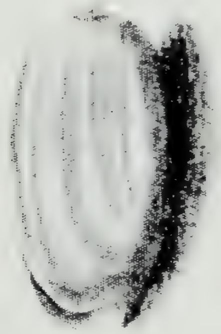
6c

Fig. 6. *Oliva nigrita* (Karsten, 1789). 6a: Martini, fig. 472. 6b: Martini, fig. 473. 6c: Martini, fig. 501. Scale 1:1.

ORIGINAL DESCRIPTION:

Voluta Nigrita Mart.

639 V.N. testa *ferruginea*, columella ex albescenti - sanguinea. 2.
Martini Konch. Kab. T.2.tab. 47.fig.501.
Long. 2 poll.1 lin. lat. 10 lin.

640 V.N. testa *ex fusco nigra* immaculata, apertura cum columella albida. Amboina, 2.
Martini loc. cit. tab. 45, fig. 472.73.
Long. 1 poll. 8 lin. lat. 10 lin.

641 V.N. testa ex fusco nigra, ad labri marginem externum *luteo striata* et characteribus obscurioribus scripta; apertura albida, columella rufescens. 2.
Long. 2 poll. 2 lin. lat.9 lin.

Note. Specimina 639-641 ad singularem speciem cum b. Martinio retuli propterea, quod columella in ipsis, postice duntaxat inprimis est striata, et magnitudine, hujus speciei omnes fere V. Olivae varietates Linn. superat.

DISCUSSION. Figures 501, 472, 473 of Martini undoubtedly refer to the shell known today as *vidua* Röding. With much reluctance we are compelled to conclude that *nigrita* Karsten is the earliest name for the well-known *vidua* Röding (of which there is no type material), which becomes an objective junior synonym as the same figs. 472 and 473 are the only illustrations cited by Röding, 1798 for *vidua*.
STATUS: **valid name**.

Note: This species is *oliva* (L., 1758) for Dautzenberg (1927), Burch & Burch (1960) and Wagner & Abbott (1978) (who consider the work non binominal).

One should also consider Karsten's *ispidula,* as this name is still available for an *Oliva,* since *ispidula* (L, 1758) has been shown not to belong to this genus). The argument used in the case of Born also applies here and the explicit reference is taken to indicate that Karsten referred to the species already described by Linnaeus.

7. The *Oliva* of Gmelin, 1791.

Two new names (*annulata* and *carneola*) were introduced by Gmelin in the 13th edition of the *Systema Naturae*. The *Oliva* of Gmelin were described as *Voluta* and in citations of these species, the name of the author should thus be enclosed in parentheses (Code, art. 51 c).

annulata (p. 3440, # 18)

ORIGINAL DESCRIPTION:

annulata. 18. V.testa laevi alba; dorsi annulo carinato.

List.Conch.t.717. f.1.

Martin. Conch. 2.t.51. f. 564.

ß) Martin. neuest. Mannigfalt., I.p.446.t.2.f.21 ?

Habitat . . . ß) rufescente undulata.

DISCUSSION. This case has been discussed in detail by TURSCH, GERMAIN & GREIFENEDER (1986) who concluded that it was a nomen dubium, used by subsequent authors to encompass both *O. amethystina* Röding and *O. mantichora* Duclos (demonstrated to be two distinct species).

The last reference of Martini will not be considered, as it was given with a question mark in the original description. The figure of Lister is very ambiguous. The "ring" alluded to by subsequent authors does not clearly show on the profile of the shell and the difference in shadowing of the body whorl could also be interpreted as indicating a difference in coloration. The figure could very well depict some other species. Fig. 564 of Martini is even more ambiguous as the details of the body whorl are suspiciously similar to those of Lister's figure. Here the shell is clearly ringed. WEINKAUFF (1878) correctly remarked "Die Martini'sche Figur kann aber ebensogut auf die gekielte und farblose Varietät der *O.peruviana* gedeutet werden". Although the shells of *O. mantichora* are frequently ringed and very occasionally occur in a white form, it would take quite a stretch of imagination to identify either *O. amethystina* Röding or *O. mantichora* Duclos with any of the above illustrations.

STATUS: **nomen dubium**.

Note: This is.

- valid for ZEIGLER & PORRECA (1969), PETUCH & SARGENT (1986).
- a form of *emicator* (Meuschen) (rejected work) for DAUTZENBERG (1927).

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carneola (p 3443, # 24)

ORIGINAL DESCRIPTION:

Carneolus. 24. V.testa aurantia : fasciis caeruleis, spira complanata et apertura albis.

Martin Conch.2.t.46.f.495.

Habitat . . .

DISCUSSION. The small coloured illustration of Martini depicts a shell with white spire, white fasciole, orange body whorl decorated with several brown horizontal stripes and a blue square blot. Although the spire and the general shape are not correctly depicted, this figure is quite compatible with the present concept of *O. carneola* (a justified subsequent correction of the original spelling *carneolus* by LAMARCK, 1811, p. 321) a name which should be preserved in the interests of stability.

Subsequent descriptions of very similar species (such as *O. kwajalainensis* da Motta, 1985).and of numerous varieties (by Dautzenberg, 1927) might eventually require the designation of a neotype.

STATUS: **valid name**.

Fig. 7. *Oliva carneola* (Gmelin, 1791). Martini, fig. 495. Scale 1:1.

---

crassa (p. 3421 # 108)

ORIGINAL DESCRIPTION:

C. testa crassa subflava : fasciis tribus albidis, ore caerulescente.

List. Conch. t. 664. f. 8.

Habitat . . . carneolae affinis, testa ultra 4 pollices longa.

DISCUSSION. This species was described in the section *Cypraea*. It is considered here only because Gmelin deemed it close to *carneola*. The figure of Lister unmistakably depicts a *Cypraea*.

STATUS: **not an *Oliva*.**

Note. This is:

- *Pseudoliva crassa* for BURCH & BURCH (1960).
- an indeterminate species for WAGNER & ABBOTT (1978).

One should also consider Gmelin's *ispidula*, this name being still available for an *Oliva* since *ispidula* (L, 1758) has been shown not to belong to this genus. The argument used in the case of Born also applies here and an explicit reference "*Mus.Lud.Ulr.*" (the *Museum Reginae Ludovicae Ulricae* of Linnaeus, 1764) indicates that Karsten refers to the species already described by Linnaeus.

"*O. leucophaea* Gmelin" is given by Mörch, 1850 and is sometimes cited in the subsequent literature. We have not found this species in Gmelin.

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8. The *Oliva* of Röding, 1798.

The *Museum Boltenianum*, written by Peter Friedrich Röding, is an inventory of the rich collection of J.F. Bolten, a leading physician in Hamburg. The rediscovery of this work at the beginning of this century and its subsequent recognition as an available work (in the sense of the Code) caused a major upset in the nomenclature of molluscs

Bolten is reported to have been a lifelong student of conchology, dissatisfied with the "crude method of Linnaeus". In contrast, we believe that his friend Röding simply intended to produce an inventory with no scientific pretensions. It can indeed be seen in the "descriptions" reported here below that he gives very accurate indications on the number (*e.g.* "15 St.") and the disposition of the specimens in the display cabinets (*Oliva* were in "*Lade*" 18 to 21) while presenting only very minimal information on the characteristics of the shells themselves. It is not surprising that the interpretation of such an inventory as a scientific publication would lead to poor results. Only 6 (less than 20%) of the 46 Röding's *Oliva* names can be identified, possibly a sad world record.

For information on the *Museum Boltenianum* see DALL (1915) and REHDER (1945).

The *Oliva* of Röding are all grouped in the genus *Porphyria*. All descriptions start with two numbers, the first -in a separate column indicates the number for the species and the second -in the text- indicates the number in the section *Porphyria*). In citations of Röding's species, the name of the author should thus be enclosed in parentheses (Code, art. 51 c).

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amethystina (p.35, # 440)

ORIGINAL DESCRIPTION:

440 | 34 P. *Amethystina*. Die amethystfarbene Dattel. Gmel.sp.23.V.ispidula. Martini 2 .t.46. f.491.492. Knorr Vergn. 2.t.10.f 6 7. 14St.

DISCUSSION. This name has already been treated in detail by TURSCH, GERMAIN and GREIFENEDER, 1986, who separated *O. amethystina* Röding, 1791 from *O. mantichora* Duclos, 1835 (so far mixed under the nomen dubium *O. annulata* Gmelin, 1791, *q.v.*).

The adjective "amethystfarbene" correctly applies to shells of the species *amethystina* many specimens of which have a deep violet colour pattern. This is very rarely (if ever) the case for shells of *mantichora*. Figures 6 and 7 of Knorr can be interpreted as depicting a specimen of *amethystina* with no markings on the suprafasciolar band. In the figures of Martini the body whorl is a rather dark yellow-beige and the interior of the aperture is deep orange. Figure 492 shows a suprafasciolar pattern compatible with the pattern characteristic of *amethystina*.

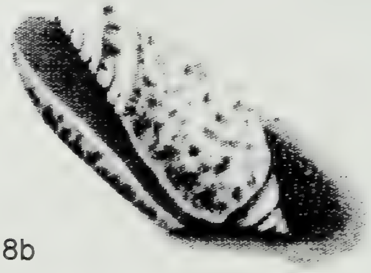
STATUS: **valid name**.

Note. This is:

- *annulata* (Gmelin, 1798) for BURCH & BURCH (1960).

a form of *annulata* (Gmelin, 1798) for WAGNER & ABBOTT (1978), ZEIGLER & PORRECA (1978), PETUCH & SARGENT (1986).
- *emicator* Meuschen (non binominal) for DAUTZENBERG (1927).

8a



8b

Fig. 8. *Oliva amethystina* (Röding, 1798). 8a: Martini, fig. 491. 8b: Martini, fig. 492. Scale 1:1.

---

amoena (p.33, # 399)

ORIGINAL DESCRIPTION:
399|13 P. *Amoena.* Die hübsche Dattel. Gmelin. V.Oliva. sp. 17. 3St.

DISCUSSION. Gmelin's sp. 17 is *oliva*, preoccupied by *oliva* (L., 1758). This name is completely unidentifiable.
STATUS: **nomen nudum**.

---

arachnoidea (p.36, # 450)

ORIGINAL DESCRIPTION:
450|43 . P. *arachnoidea.* Die Spinneweben-Dattel. Gmel. V.Oliva α. sp. 17. Martini 2.t.48.f.509.10. 1St.

DISCUSSION. Martini's figures were both utilised by Röding himself for *spicata*. As *spicata* is a name in very common use it should be preserved in the interests of stability.
STATUS: **objective synonym** of ***spicata*** (Röding, 1798).

---

aurata (p. 33, # 402)

ORIGINAL DESCRIPTION:
402|16 P. *aurata.* Die goldgelbe Dattel. Gmel. V.Oliva .sp. 17. 1St.
DISCUSSION. Gmelin's sp. 17 is *oliva*, preoccupied by *oliva* (L., 1758). This name is completely unidentifiable.
STATUS: **nomen nudum**.

Note. This is:
- a variety of *oliva* (L., 1758) for DAUTZENBERG (1927).
- *oliva* (L., 1758) according to BURCH & BURCH (1960).
- a colour form of *vidua* (Röding, 1798) for ZEIGLER & PORRECA (1969), WAGNER & ABBOTT (1978) and PETUCH & SARGENT (1986).

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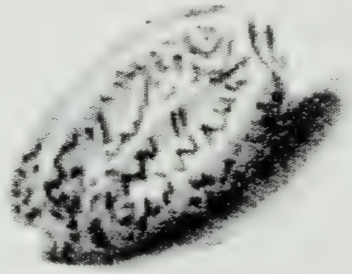
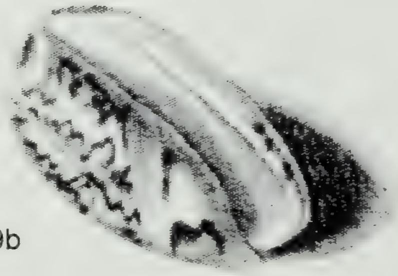
bulbosa (p. 37, # 459)



9a



9b

Fig. 9. *Oliva bulbosa* (Röding, 1798). 9a: Martini, fig. 507. 9b: Martini, fig. 508. Scale 1:1.

ORIGINAL DESCRIPTION:

459|50 P. *Bulbosa.* Die knolligte Dattel. Gmel.sp. 17. Oliva ζ. Martini 2.t.47 .f.507.508. 2St.

DISCUSSION. Martini's figures 507 and 508 were previously utilised by Gmelin for *oliva*, a name preoccupied by *oliva* (L., 1758). The two figures are quite compatible with the present concept of *O. bulbosa*, a name that should be preserved in the interests of stability. The drawing of the columella rather vaguely suggests the characteristic prominent columellar plications of the species and the adjective "knolligte" could be taken to refer to this peculiarity.

STATUS: **valid name**.

---

caerulea (p. 33, # 392)

ORIGINAL DESCRIPTION:

392|7 P. *Caerulea.* Die himmelblaue Dattel. Gmel.V.Oliva sp. 17.α. Martinii 2.t.48.f. 518. Rumph. t.39. f.5. 13 St.

DISCUSSION. This case has already been studied by KILBURN (1980). The figure of Martini was previously used for *oliva* var. of Gmelin. Gmelin's sp. 17 is *oliva*, preoccupied by *oliva* (L., 1758). The figure (designated as a type figure by KILBURN) shows a characteristic blue colour aperture and is quite compatible with the present concept of *O. caerulea.*

STATUS: **valid name**.

Fig. 10. *Oliva caerulea* (Röding, 1798). Martini, fig. 518. Scale 1:1.

Note. This is:

- *episcopalis* Lamarck, 1811 for DAUTZENBERG (1927), BURCH & BURCH (1960) and ZEIGLER & PORRECA (1969).

---

cornea (p. 36, # 448)

ORIGINAL DESCRIPTION:

448|41. P. cornea. Die hornfarbene Dattel. 1 St.

DISCUSSION. This species is completely unidentifiable.

STATUS: **nomen nudum**.

---

cingulata (p. 34, # 415)

ORIGINAL DESCRIPTION:

415|21 P. *Cingulata.* Die gegürtelte Dattel. Gmel.V.Oliva sp. 17. 1St.

DISCUSSION. Gmelin's sp. 17 is *oliva*, preoccupied by *oliva* L., 1758. This name is completely unidentifiable.

STATUS: **nomen nudum**

Note. This is *annulata* (Gmelin, 1791) for WAGNER & ABBOTT (1978).

---

coffea (p. 37, # 462)

ORIGINAL DESCRIPTION:

462|53 P. *Coffea.* Die Kaffeebohne. Gmel.sp.24. V.carneolus. Martini 2.t.46. f.495. 4St.

DISCUSSION. Martini's figure 495 was previously utilised by Gmelin for *carneola*, cited by Röding.

STATUS: **objective junior synonym** of ***carneola*** Gmelin, 1791.

Note. This is indeterminate, possibly *oliva* (L., 1758) for WAGNER & ABBOTT (1978).

---

conoidea (p. 35, # 430)

ORIGINAL DESCRIPTION:

430|31 P. *Conoidea.* Die kegelförmige Dattel. 1St.

DISCUSSION. This name is completely unidentifiable.

STATUS: **nomen nudum**.

---

dealbata (p. 35, # 427)

ORIGINAL DESCRIPTION:

427 | 29 P. *Dealbata.* Die schneeweisse Dattel. Knorr 6. t. 34. f. 4 5. 6 St.

α 1 St.

DISCUSSION. Knorr's figures (on a black background) are compatible with an all-white specimen of the "*O. oliva* complex" shown to be composed of distinct, closely related species (TURSCH, MISSA & BOUILLON, 1992) well separated by multivariate analysis but impossible to segregate on the basis of approximate illustrations.

STATUS: **nomen dubium**.

Note. This is a white form of *oliva* (L., 1758) for WAGNER & ABBOTT (1978) and PETUCH & SARGENT (1986).

The name *fasciata* was used twice, for two different shells (sp. 387 and sp. 411).

fasciata (p. 32, # 387)

ORIGINAL DESCRIPTION:

387 | 2 P. *Fasciata.* Die gebandete Portobello-Dattel. Gmel. Voluta sp. 16 γ. 1St.

DISCUSSION. Gmelin's sp. 16 is *porphyria*, preoccupied by *porphyria* (L., 1758). One should note that Röding also uses "Portobello-Dattel" for *porphyria* (species 386). The adjective "gebandete" indicates that Röding means a banded colour variation of this shell. There is no indication whatsoever that such a variant would deserve specific or subspecific status.

STATUS: **subjective junior synonym** of ***porphyria*** (L., 1758).

---

fasciata (p. 34, # 411)

ORIGINAL DESCRIPTION:

411 | 19 P. *Fasciata.* Die Band Dattel. Gmel.V.sp. 17. Knorr 3.t.17 .f.3. 6St.

DISCUSSION. Knorr's figure was previously utilised by Gmelin for *oliva*, preoccupied by *oliva* (L.,1758). The very fact that the name *fasciata* was used twice (apparently for very different shells) casts a serious doubt upon Röding's nomenclatural concepts. The figure of Knorr is easily recognisable as the dark form of *nigrita* Karsten, 1789, also described as *vidua* by Röding.

STATUS: **junior homonym** of ***fasciata*** (sp. 387 Röding.,1798) to which we give page precedence.

Note. This is:

- *oliva* (L., 1758) for BURCH & BURCH (1960).
- *reticulata* (Röding, 1798) for WAGNER & ABBOTT (1978).

---

fenestrata (p. 34, # 417)

ORIGINAL DESCRIPTION:

417 | 22 . P. *Fenestrata.* Die gegitterte Dattel. Gmel.V.Oliva sp. 17 ß. Martini 2.t.47 .f.502. 2St.

DISCUSSION. Martini's figure was previously used by Gmelin for *oliva*, preoccupied by *oliva* (L., 1758). This colour figure (vaguely reminiscent of a golden form of *vidua* by the same author) presents a very strange cross-ruled pattern (never seen by us in an *Oliva*). It is not recognisable with any certainty.

STATUS: **nomen dubium.**

Note. This is a form of *vidua* (Röding, 1798) according to DAUTZENBERG (1927), ZEIGLER & PORRECA (1969), WAGNER & ABBOTT (1978) and PETUCH & SARGENT (1986).

---

fimbriata (p.34, # 410)

ORIGINAL DESCRIPTION:

410 | 18 P. *Fimbriata.* Eine schöne rostfarbigte Dattel mit dem Saum. 1St.

DISCUSSION. One should note that *fimbriata* was presented together with *oliva* under 410. This name is completely unidentifiable.

STATUS: **nomen nudum**.

---

fulgurator (p.36, # 453)

ORIGINAL DESCRIPTION:

453 | 45 P. *Fulgurator.* Die Blitz-Dattel. Gmel.sp. 17.V.oliva α. Martini 2.t.51. f.562. 14St.

DISCUSSION. Martini's figure 562 was previously utilised by Gmelin for *oliva* var., a name previously preoccupied by *oliva* (L., 1758). The figure is very recognisable and

depicts a specimen of *fulgurator* in the presently accepted sense of the name.
STATUS: **valid name.**

Fig. 11. ***Oliva fulgurator*** (Röding, 1798). Martini, fig. 562. Scale 1:1.

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griseola (p.35, # 424)

ORIGINAL DESCRIPTION:

424 | 26 P. *Griseola*. Die gräuliche Dattel. 3St.

DISCUSSION. This name is completely unidentifiable.
STATUS: **nomen nudum**.

---

hepatica (p.33, # 400)

ORIGINAL DESCRIPTION:

400 | 14 P. *Hepatica*. Die lichtgraue Dattel. Gmel. V.Oliva. sp. 17. 2St.

DISCUSSION. Gmelin's sp. 17 is *oliva*, preoccupied by *oliva* Linnaeus, 1758. This name is completely unidentifiable.
STATUS: **nomen nudum**.

---

isabella (p.33, # 401)

ORIGINAL DESCRIPTION:

401 | 15 P. *Isabella*. Die isabellfarbene Dattel. Gmel. V.Oliva. sp. 17. 3St.

DISCUSSION. Gmelin's sp. 17 is *oliva*, preoccupied by *oliva* (L., 1758). This name is completely unidentifiable.
STATUS: **nomen nudum**.

---

ispida (p.35, # 431)

ORIGINAL DESCRIPTION:

431 | 32 P. *Ispida* Die blaumündige Dattel. Gmel Voluta sp.23. Martini 2.t.49. f.524.25.30. Knorr 3.t.19.f.3. 21 St.

432	α	Mart. 2. t.49. f.535. 3St.
433	ß	Martini 2.t.49. f.522.23. 5St.
434	γ	4 St.
435	δ	3 St.

DISCUSSION. Martini's figures 522, 523, 524 as well as Knorr's fig. 19/3 were previously utilised by Gmelin for *ispidula*, a name preoccupied by *ispidula* Linnaeus, 1758. Martini's figures 525 , 530 and 535 were not previously utilised. All the figures are compatible with specimens of the "*Oliva oliva* complex" shown to be composed of distinct, closely related species (TURSCH, MISSA & BOUILLON, 1992) well separated by multivariate analysis but impossible to segregate on the basis of approximate illustrations.
STATUS: **nomen dubium.**

Note. This is:
- a *nomen nudum* according to BURCH & BURCH (1960).
- *oliva* (L., 1758) for ZEIGLER & PORRECA (1969), WAGNER & ABBOTT (1978) and PETUCH & SARGENT (1986).

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labradoriensis (p.32, # 389)

ORIGINAL DESCRIPTION:

389 | 4 P. *Labradorensis*. De Schiller-Dattel. Gmel. Voluta Oliva, sp. 17.. Lister 731. f.20. 2 St.

DISCUSSION. The figure of Lister was previously utilised by Gmelin in conjunction with *oliva*, a name preoccupied by *oliva* (L., 1758). It was later utilised by Lamarck for *mustelina*. The figure is not recognisable and possibly depicts an *Agaronia*.
STATUS: **nomen dubium**.

Note. This (misspelled "*labradorensis*") is:
a *nomen nudum* according to BURCH & BURCH (1960).

- possibly *funebralis* Lamarck, 1811 for PETUCH & SARGENT (1986).

---

litterata (p.36, # 452)

ORIGINAL DESCRIPTION:

452 | 44 P. *Litterata.* Die Buchstaben - Dattel. Gmel.sp. 17. V.oliva.γγ. Martini 2.t.46. f.488. 14 St.

DISCUSSION. Martini's figure 488 was previously utilised by Gmelin for *oliva* var., a name preoccupied by *oliva* (L., 1758). It is not recognisable and could amongst others represent either *spicata*, *reticularis* or *fulgurator*.
STATUS: **nomen dubium**.

Note. This is *spicata* (Röding, 1798) according to BURCH & BURCH (1960), WAGNER & ABBOTT (1978), ZEIGLER & PORRECA (1969), KEEN (1971) and PETUCH & SARGENT (1986).

---

mica (p.35, # 436)

ORIGINAL DESCRIPTION:

436 | 33 P. *Mica.* Die blaugefleckte Dattel. Gmel. sp.23. V.ispidula. 23 St.
437 | α Martini 2.t.49 f.527-529. 3 St.
438 | β 10 St.
439 | γ 3 St.

DISCUSSION. Martini's figures were never utilised before. These figures represent an unidentifiable Olive, with a very strange lip, possibly a freak.
STATUS:.**nomen dubium.**

Note. This is *oliva* (L., 1758) according to WAGNER & ABBOTT (1978) and PETUCH & SARGENT (1986).

---

miniacea (p.33, # 391)

ORIGINAL DESCRIPTION:

391 | 6 P. *Miniacea.* Das Morgenroth. Gmelin V. porphyria. sp.16 ß. Martini 2.t.45. f.476,477. 9 St.

DISCUSSION. Both figures of Martini were previously used for *porphyria* Gmelin, a name preoccupied by *porphyria* (L., 1758). The figures are highly recognisable and depict the present, widely utilised concept of *miniacea*. The same figures were utilised later by Lamarck for *erythrostoma*.
STATUS: **valid name.**

Note. This is: *erythrostoma* Meuschen (rejected work) for DAUTZENBERG (1927).

Fig. 12. ***Oliva miniacea*** (Röding, 1798). 12a: Martini, fig. 476. 12b: Martini, fig. 477. Scale 1:1.

---

oculata (p.35, # 426)

ORIGINAL DESCRIPTION:

426|28 P. *Oculata* Die geängelte Dattel. 12 St.

DISCUSSION. "Geängelte" is probalbly a misprint for "geäugelte". This name is completely unidentifiable.

STATUS: **nomen nudum**.

---

ornata (p.33, # 398)

ORIGINAL DESCRIPTION:

398|12 P. *Ornata* Die geschmüekte Dattel. Gmel. V.Oliva. sp. 17. 2 St.

DISCUSSION. Gmelin's *oliva* is preoccupied by *oliva* (L., 1758). This species is completely indeterminate.

STATUS: **nomen nudum**.

Note. This is *oliva* (L., 1758) according to WAGNER & ABBOTT (1978).

---

paleacea (p.36, # 442)

ORIGINAL DESCRIPTION:

442|36 P. *Paleacea.* Die strohfarbene Dattel. 1 St.

DISCUSSION. This name is completely unidentifiable.

STATUS: **nomen nudum**.

---

papyracea (p. 36, # 443)

ORIGINAL DESCRIPTION:

443|37 P. *Papyracea.* Die buntpapierne Dattel. 4 St.

DISCUSSION. This name is completely unidentifiable.

STATUS: **nomen nudum**.

---

punctata (p.33, # 397)

ORIGINAL DESCRIPTION:

397|11 P. *Punctata.* Die gestippelte Dattel. Gmel. V.Oliva. sp. 17. 4 St.

DISCUSSION. Gmelin's *oliva* is preoccupied by *oliva* (L., 1758). This name is completely unidentifiable.

STATUS: **nomen nudum**.

Note. This is:

-*spicata* (Röding, 1798) var. *venulata* Lamarck, 1811 according to BURCH & BURCH (1960).

-*oliva* (L., 1758) for WAGNER & ABBOTT (1978) and PETUCH & SARGENT (1986).

- *rejecta* Burch & Burch, 1962 according to PETUCH & SARGENT (1986)

---

quercina (p.34, # 418)

ORIGINAL DESCRIPTION:

418|23 P. *Quercina.* Die Eichenholz - Dattel. Gmel. V.Oliva sp. 17.
Knorr 5.tab.26. fig.4. 6 St.
419| P. α 2 St.
420| β Knorr 5.t.27.fig.5. 1 St.

DISCUSSION. Knorr's fig. 26/4 was previously utilised by Gmelin for *oliva* var. and by Röding himself for *sepultura principis.* Knorr's fig. 27/5 was previously utilised by Gmelin for *oliva* var., preoccupied by *oliva* (L., 1758). Many olives with a low spire have melanistic forms and these figures are ambiguous.

STATUS: **nomen dubium**.

Note. This could be *reticulata* (Röding, 1798) for WAGNER & ABBOTT (1978).

---

reticulata (p.33, # 396)

ORIGINAL DESCRIPTION:

396|10 P. *Reticulata.* Die Netz-Dattel. Gmel.V.Oliva.sp. 17.α. Martini 2.t.48. f.512.533. 9 St.

DISCUSSION. Martini's figure 512 was previously utilised for *oliva* as well as *ispidula* Gmelin (both names preoccupied by Linnaeus). It was later utilised for *sanguinolenta* Lamarck. Fig. 533 was not previously utilised. It was used later by Lamarck for *fabagina.* Fig. 533 is entirely unidentifiable (and "533" is probably a misprint for 513), but Fig. 512 (a dark brow-grey shell with an orange columella and lip) is not inconsistent with the current acceptation of the widely used name *reticulata,* which should be kept for the sake of stability.

STATUS:.**valid name.**

Note. This is *sanguinolenta* Lamarck, 1811 for BURCH & BURCH (1960).

Fig. 13. *Oliva reticulata* (Röding, 1798). Martini, fig. 512. Scale 1:1.

---

ruffina (p.32, # 388)

ORIGINAL DESCRIPTION:

388 | 3 P. *Ruffina.* Die rothe Dattel. Gmel.Vol. sp.49.γ. 2 St.

DISCUSSION. There is a previous *V. ruffina* of Gmelin (p. 3450, sp. 49) which is not cited by Röding. It is based upon "Gualtieri t.54 f. G ?". This figure could depict *vidua*, but Gmelin's decription of *ruffina* "... *V. testa integriuscula transversim rugosa: columella quadriplicata, labro crenulato*" is not compatible with an *Oliva*. Röding's *ruffina* is completely unidentifiable.

STATUS: **nomen dubium**.

Note. This is a *nomen nudum* for WAGNER & ABBOTT (1978).

---

sepultura principis (p.33, # 403)

ORIGINAL DESCRIPTION:

403 | 17 P. *Sepultura Principis.* Das Prinzen Begräbnisz. Gmel.V.Oliva.sp. 17.ξ. Rumpf t.39.f.4.

α 2 St.

405 | β Martini 2.t.51.f.563. Knorr 5.t.26.f.4. 4 St.

406 | γ Martini 2.t.45.f.480.481. Knorr 5.t.19.f.1. 3 St.

407 | δ 4 St.

408 | ε 2 St.

409 | ξ 1 St.

DISCUSSION. The figure of Rumphius was previously utilised by Gmelin for *oliva*. Knorr's fig. 26/4 was previously utilised by Gmelin for *oliva* var. and was also utilised by Röding himself for *quercina*. Knorr's fig. 19/1 was previously utilised by Gmelin for *oliva* var. and was also utilised by Röding himself for *variegata* α. Martini's figs. 45/480, 481 were previously utilised by Gmelin for *oliva* var. and are utilised later by Lamarck for *funebralis*. Martini's fig. 51/563 was previously utilised by Gmelin for *oliva* var. Gmelin's *oliva* is preoccupied by Linnaeus, 1758. Knorr 5.t.19.f.1. is a *Conus* (possibly *aulicus*). Martini 2.t.51.f.563 is ambiguous, could be *peruviana* as well as *vidua*. Martini 2.t.45.f.480.481 could be what we call *Oliva funebralis*. Rumpf. t.39.f.4. is not recognisable. Knorr 5.t.26.f.4. is reminiscent of the shell now usually called *lignaria*, but could be any dark olive with a low, calloused spire. All these figures are either unidentifiable or conflicting.

STATUS: **nomen dubium.**

Note. This could be *funebralis* Lamarck,1811 for WAGNER & ABBOTT (1978).

---

sericea (p.33, # 390)

ORIGINAL DESCRIPTION:

390 | 5 P. *Sericea.* Das Seidenzeug. Gmel. V.oliva sp. 17.δδ. Martini 2.t.51. f.559.561. 8 St.

DISCUSSION. Martini fig.559 previously utilised for *oliva* var. Gmelin, later by Lamarck for *textilina*. Fig. 561 later utilised by Lamarck for both *irisans* and *reticularis*. Gmelin's sp. 17 is *oliva*, a name preoccupied by Linnaeus. The figures are not inconsistent with the current acceptation of the widely used name *sericea*, which should be kept for the sake of nomenclatural stability.

STATUS: **valid name**.

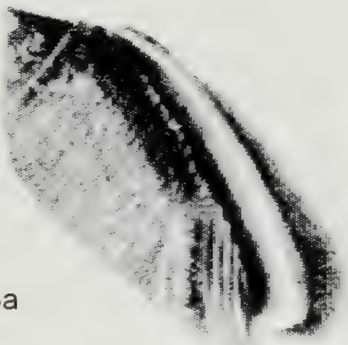
Note. This is:

- *textilina* Lamarck, 1811 for DAUTZENBERG (1927)
- *textilina* Lamarck, 1811 (*pars*) for BURCH & BURCH (1960) and ZEIGLER & PORRECA (1969).

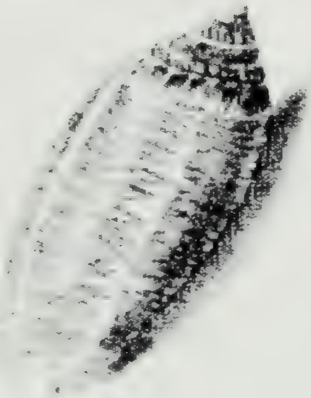
14a

14b

Fig. 14. *Oliva sericea* (Röding, 1798). 14a: Martini, fig. 559. 14b: Martini, fig. 561. Scale 1:1.



15a



15b

Fig. 15. *Oliva spicata* (Röding, 1798). 15a: Martini, fig. 509. 15b: Martini, fig. 510. Scale 1:1.

spicata (p.35, # 423)

ORIGINAL DESCRIPTION:

423 | 25 P. *Spicata* Die Kornähre. Gmel.V.oliva sp. 17. Martini 2.t.48. f.509.10. 7 St.

DISCUSSION. Martini's figures were previously utilised by Gmelin for *oliva*, preoccupied by *oliva* (L., 1758). The same figures are utilised by Röding himself for *arachnoides*. They were later utilised by Lamarck for *araneosa*. The figures are not inconsistent with the current acceptation and the widely used name *spicata* should be kept for the sake of stability.

STATUS: **valid name.**

Note. "*O. intertincta* Röding, 1798" given in the synonymy of *spicata* by WAGNER & ABBOTT (1978) is not a name published by Röding. Probably a typographic error for *intercincta* Carpenter, 1857.

textilis (p.37, # 456)

ORIGINAL DESCRIPTION:

456 | 47 P. *Textilis.* Die gewebte Dattel. 1 St.

DISCUSSION. This name is completely unidentifiable.

STATUS: **nomen nudum**.

tigris (p.36, # 441)

ORIGINAL DESCRIPTION:

441 | 35 P. *Tigris.* Die Tiger-Dattel. 1 St.

DISCUSSION. This name is completely unidentifiable.

STATUS: **nomen nudum**.

tuberosa (p.37, # 460)

ORIGINAL DESCRIPTION:

460|51 P. *Tuberosa* Die kanehlfarbene Dattel. Kammerer t.3.fig. 7.8. 3 St.

DISCUSSION. Kammerer's figures are quite clear and unmistakably depict a form of *O. bulbosa* (Röding, 1798), a conclusion also reached by WAGNER & ABBOTT (1978), ZEIGLER & PORRECA (1969) and PETUCH & SARGENT (1986). The name *bulbosa* has page precedence, is widely used and should be kept for the sake of stability.
STATUS: **subjective junior synonym** of ***bulbosa*** (Röding, 1798).

---

tumida (p.37, # 455)

ORIGINAL DESCRIPTION:

455|46 P. *Tumida.* Die aufgeblasene Dattel. Lister t.746.f.40. 1 St.

DISCUSSION. Lister's figure 40 was previously utilised by Gmelin in his remarks on *oliva*, a name preoccupied by *oliva* (L., 1758). The figure of Lister is unrecognizable and might even not depict an *Oliva*. This name is completely unidentifiable.
STATUS: **nomen nudum.**

Note. This is an indeterminate *Ancilla* for WAGNER & ABBOTT (1978).

---

turgida (p.34, # 416)

ORIGINAL DESCRIPTION:

416|21 * B. *Turgida* Die wulstige Dattel. Gmel. V.Oliva sp. 17. 1 St.

DISCUSSION. We have no explanation for the "* B." in the original description. It might be a typographical error. Gmelin's sp. 17 is *oliva*, a name preoccupied by *oliva* (L., 1758). This name is completely unidentifiable.
STATUS: **nomen nudum**.

---

umbrosa (p.36, # 449)

ORIGINAL DESCRIPTION:

449|42 P. *Umbrosa.* Die Licht- und Schatten-Dattel. Gmel.Voluta ispidula α. sp.23. Martini 2.t.49.f.537. Knorr 1.t.15. f.7. 3 St.

DISCUSSION. Martini's figure 537 was never utilised before. Knorr's figure 7 was utilised by Gmelin for *oliva*, a name preoccupied by *oliva* (L., 1758). The figures of Martini and Knorr are compatible with a dark specimen of the "*Oliva oliva* complex" shown to be composed of distinct, closely related species (TURSCH, MISSA & BOUILLON, 1992), well separated by multivariate analysis but impossible to segregate on the basis of approximate illustrations.
STATUS: **nomen dubium.**

Note. This is *oliva* (L., 1758) for WAGNER & ABBOTT (1978) and PETUCH & SARGENT (1986)

---

undulata (p.35, # 425)

ORIGINAL DESCRIPTION:

425|27 P. *Undulata* Die wellenförmige Dattel. 18 St.

DISCUSSION. This name is completely unidentifiable.
STATUS: **nomen nudum**.

---

variabilis (p.33, # 395)

ORIGINAL DESCRIPTION:

395|9 P. *Variabilis.* Die spielende Dattel. Gmel. V. Oliva.p.17. 7 St.

DISCUSSION. Gmelin's sp. 17 is *oliva*, a name preoccupied by *oliva* (L., 1758). This name is completely unidentifiable.
STATUS: **nomen nudum.**

Note. This is:
- *sanguinolenta* Lamarck, 1811 for BURCH & BURCH (1960).
- *reticulata* (Röding, 1798) for WAGNER & ABBOTT (1978), ZEIGLER & PORRECA (1969) and PETUCH & SARGENT (1986).

---

variegata (p.33, # 393)

ORIGINAL DESCRIPTION:

393|8 P. *Variegata.* Die schäckigte Dattel. Gmel.Voluta.Sp. 17.δ. Martini 2.t.45.f.478.479. 24 St.
394| α Martini 2.t.45.f.480.481. Knorr 5.t.19.f.1. 5 St.

DISCUSSION. Martini's fig. 478 and 479 were previously utilised by Gmelin for *oliva.* Martini's figs. 480 and 481 were utilised by Gmelin for a variety of *oliva*, by Röding himself for *sepultura principis* (a nomen dubium) and later by Lamarck for *funebralis.* Knorr's figure (possibly *Conus aulicus*) had already been utilised for *oliva* and *oliva* var. by Gmelin; and also by Röding himself for *sepultura principis.* Gmelin's sp. 17 is *oliva* a name preoccupied by *oliva* (L., 1758).
STATUS: **nomen dubium.**

Note. This is:
- *sanguinolenta* Lam., 1811 for DAUTZENBERG (1927).
- *reticulata* (Röding, 1798) for WAGNER & ABBOTT (1978), ZEIGLER & PORRECA (1969), PETUCH & SARGENT (1986).

---

vellus-aureum (p.36, # 444)

ORIGINAL DESCRIPTION:
444 | 38 P. *Vellus-aureum.* Das goldne Vliesz. Gmel.V.Oliva sp. 17.var.εε. Martini 2.t.46.f.490. 3 St.

DISCUSSION. Martini's fig. 490 was previously utilised by Gmelin for *oliva* var., a name preoccupied by *oliva* (L., 1758). The figure could represent *reticularis* as well as *spicata* or even another species.
STATUS: **nomen dubium.**

Note. This is probably *oliva* (L., 1758) for WAGNER & ABBOTT (1978)

---

vidua (p.34, # 412)

ORIGINAL DESCRIPTION:
412 | 20 P. *Vidua* Die ungarische Wittwe. Gmel.V.sp. 17. Martini 2.t.45. f.472.473. 17 St.
413 | α 1 St.
414 | β 1 St.

DISCUSSION. Martini's figures have been previously utilised by Gmelin for *oliva*, a name preoccupied by Linnaeus, 1758. They were later utilised by Lamarck for *maura.* As both cited figures were utilised to establish *nigrita* (Karsten, 1789) we are reluctantly compelled to give priority to Karsten's name.

STATUS: **objective junior synonym** of ***nigrita*** Karsten, 1789.

Note. This name is *valid* according to BURCH & BURCH (1960), ZEIGLER & PORRECA (1969) PETUCH & SARGENT (1986).

---

ziczac (p.37, # 461)

ORIGINAL DESCRIPTION:
461 | 52 P. *Ziczac.* Die Ziczac Dattel. 4 St.

DISCUSSION. This name is completely unidentifiable.
STATUS: **nomen nudum**.

---

9. The *Oliva* of Link, 1807.

In his *Beschreibung*, Link introduces the new names *coerulea* (not *caerulea*), *fusca, miniata, taeniata* and *tentorium.* The name *aurata* also has to be considered, since *aurata* (Röding, 1798) is a *nomen nudum* and therefore remains available.
The *Oliva* of Link are all grouped in the genus *Porphyria*, and in citations of these species, the name of the author should thus been enclosed in parentheses (Code, art. 51 c).

aurata (p. 97)

ORIGINAL DESCRIPTION:
P. *aurata.* Gelbmündige D. Mart.Conch. 2.t.46.f.491,492. Unterscheidet sich von allen übringen durch die gelbe Mündung; nähert sich sonst in allen Stücken sehr der vorigen (note: this refers to *coerulea*).

DISCUSSION. The two Martini figures have already been used by Röding for *amethystina.*
STATUS: **objective junior synonym** of ***amethystina*** (Röding, 1798).
Note. This is a color form of *bulbosa* (Röding, 1798) for PETUCH & SARGENT (1986)

---

coerulea (p. 97)

ORIGINAL DESCRIPTION:
P. *coerulea.* Kamelot D. Bolt. Verz. p. 33. γ. Oliva α. Linn. Gm. I. c. Mart. Conch. 2. t. 48. f. 515. 516. Unterscheidet sich von allen übrigen durch die blaue Mündung, auch ist viel Blau in

der Zeichnung. Die Grösse ist nicht viel über ein Zoll; die kleinern weichen etwas in der Form ab. Die zweite Windung ist wenig oder gar nicht aufwärts getrümmt. Immer ist sie schmal.

DISCUSSION. Although the cited figures of Martini are not convincing, the explicit reference to the Bolten Catalogue and the description point to *caerulea* (Röding, 1798).
STATUS: **incorrect spelling** for ***caerulea*** (Röding, 1798).

---

fusca (p. 95)

ORIGINAL DESCRIPTION:
P. *fusca*. Zigeuner D. V.Oliva ε Linn.Gm.l.c. Mart. Conch.2.t.47. f.501. Gelblich braun; die zweite Mündung stark aufwärts gebogen.

DISCUSSION. *O. fusca* (Link, 1807) is a homonym of *fusca* Fischer, 1807. We know the exact date of publication neither of the *Museum Demidoff* (Fischer, 1807) nor of the *Beschreibung* (Link, 1807) and we are thus unable to decide on priority. The Martini figure had already been used for a variety of *O. oliva* by Gmelin. This figure depicts the orange variety of *nigrita* (Karsten, 1789) (see Pl. 9, fig. 3 of Zeigler & Porreca, as *vidua* Röding, 1798).
STATUS: **subjective junior synonym**.of ***nigrita*** (Karsten, 1789).

Note. This is:
- *oliva* (L., 1758) for BURCH & BURCH (1960).
- *vidua* (Röding, 1798) for WAGNER & ABBOTT (1978), PETUCH & SARGENT (1986).

---

miniata (p. 95)

ORIGINAL DESCRIPTION:
P. *miniata*. Morgenroth D. Bolt. Verz. p.33. Porphyria ß Linn.l.c. Mart. Conch. 2. t.45. f.476.477. Kenntlich an der rothen Mündung.

DISCUSSION. Both Martini figures had already been used by Röding for *miniacea*.
STATUS: ***objective junior synonym*** of ***miniacea*** (Röding, 1798).

---

taeniata (p. 98)

ORIGINAL DESCRIPTION:
P. *taeniata*. Bandirte D. Mart. Conch. 2. t.49. f.530. Vielleicht nur eine Abänderung der vorigen (this is *ispidula*), von der sie sich allein durch das dunkle, einfarbige Querband am obern Ende der ersten Windung unterscheidet.

DISCUSSION. The Martini figure had already been used by Röding for *ispida*.
STATUS: **objective junior synonym** of ***ispida*** (Röding, 1798).

Note. This is:
- *ispidula* (L., 1758) according to BURCH & BURCH (1960).
- a form of *oliva* (L., 1758) for WAGNER & ABBOTT (1978) and ZEIGLER & PORRECA (1969).
- a subspecies of *oliva* (L., 1758) for PETUCH & SARGENT (1986)

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tentorium (p. 95)

ORIGINAL DESCRIPTION:
P. *tentorium*. Portobello D. V.Porphyria Linn. Gm.p.3438. Mart. Conch.2 .t.46. f.485.486. Das türkische Zelt.

DISCUSSION. One should note that Röding also used the vernacular "Portobello-Dattel" for *porphyria* (species 386). Both Martini figures clearly depict *porphyria* (L., 1758) and had indeed been utilised in the original description by Linnaeus.
STATUS: **objective junior synonym** of ***porphyria*** (L., 1758).

Note. This is spelled "*tentoria*" by BURCH & BURCH (1960) and PETUCH & SARGENT (1986).

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10. The *Oliva* of Fischer, 1807.

G. Fischer von Waldheim described in the *Museum Demidoff* (in French) a collection given by Paul de Demidoff to the Imperial University of Moscow. This collection, long thought lost during the siege of Moscow by Napoleon, has been recently retrieved (IVANOV &KANTOR, 1991).

The species considered new by Fischer are marked by "*m.*" or "*mihi*". Fischer is the first author to have placed all his species in the genus *Oliva*. Fischer, a generally accepted author, appears however not to be consistently binominal, describing some species (*e.g.* the "Olive lettrée" only by vernacular names).

fusca (p. 160, # 19-30)

ORIGINAL DESCRIPTION:

19. 20. L'olive nègre, unie; la base de la spire recourbée, la columelle obliquement striée.

Oliva fusca m.

Voluta oliva Lin. Gm. 3439.17. Bosc.5.37. Martini 2.t.45.f.472-473. Knorr.5.t.28.f.6. - se touve dans la mer des *Indes*.

21. β. l' **Olive** à robe brune plus claire avec des raies transversales plus foncées.

22-25. γ. l' *Olive* à robe brun - clair passant au rouge ou au jaune.

26. δ. l' **Olive** à robe brune avec une bande ou zone, au milieu, tachetée de noir.

27. 28. ε. l' **Olive** brune à stries longitudinales plus foncées.

29. ζ. l' **Olive** blanchâtre avec des taches irrégulières couleur d' olive.

30. ϑ. l' Olive verdâtre avec des desseins en zigzag.

DISCUSSION. *O. fusca* Fischer, 1807 is a homonym of *fusca* (Link, 1807). We know the exact date of publication neither of the *Museum Demidoff* (Fischer, 1807) nor of the *Beschreibung* (Link, 1807) and we are thus unable to decide on priority. Bosc refers to a vast assortment of entirely unrelated Olives. This species is represented in Moscow by a series. The lectotype selected by IVANOV & KANTOR (1991) was identified as *vidua* (Röding, 1798), an objective junior synonym of *nigrita* (Karsten, 1789).

STATUS: **subjective junior synonym** of ***nigrita*** (Karsten, 1789).

Note. This is *oliva* (L., 1758) according to BURCH & BURCH (1960) and WAGNER & ABBOTT (1978).

---

guttata (p.162, # 133)

ORIGINAL DESCRIPTION:

133. **Olive Girol**, Alongée, lisse, la spire courte et lisse, la bouche très ouverte et violette.

Oliva guttata mihi. Elle a été figurée par Lister 720.6. Martini 2. p. 161. t. 46. 493. 494. le ***Girol*** d' Adanson p. 61. Pl. 4. f. 6. -La partie en est inconue.

DISCUSSION. The specimen of *guttata* in the collection is said to have been lost before 1872 (IVANOV, D.L. & Yu. KANTOR, 1991). The figure of Adanson is not clearly recognisable. Figs. 472-473 of Martini were utilised for *olivacea* (Karsten, 1789), an earlier name for *tessellata* Lamarck, 1811 (who indeed refers to the same figures). The figure of Lister, as well as the description agree with that identification.

STATUS: **objective junior synonym** of ***olivacea*** (Karsten, 1789).

Note. This is:

- *annulata* (Gmelin, 1791) according to BURCH & BURCH (1960) and WAGNER & ABBOTT (1978).
- a color form of *annulata* (Gmelin, 1791) for PETUCH & SARGENT (1986).

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plicata (p. 161, # 90-92)

ORIGINAL DESCRIPTION:

90. L'olive bossue Ovale unie, le second tour de la spire enfoncé, trois plis distincts de la columelle, dont le premier très élevé.

Oliva plicata mihi. Je n'en connois pas de figure.

Elle est ovale, blanche ou verdâtre, ponctuée de brun de différente manière. La lèvre est épaisse, distante dans toute sa longueur.

Elle est de la grandeur de l' *Olive nègre*.

91. Variété de la même, jaune ponctuée de brun.

La patrie en est inconnue.

DISCUSSION. The specimen of *plicata* in the collection is said to have been lost before 1872 (IVANOV & KANTOR, 1991). This name is unidentifiable and might even not apply to an *Oliva*.

STATUS: **nomen dubium**.

One should also consider Fischer's *ispidula*, this name being still available for an *Oliva* since *ispidula* (L, 1758) has been shown not to belong to this genus). The specimen of *ispidula* in the collection is said to have been lost before 1872 (IVANOV & KANTOR, 1991). The argument used in the case of Born also applies here. The first reference for this species is "*Voluta ispidula* Gmel. 3442. n. 23". This is *ispidula* L.and it can be concluded that Fischer refers to the species already described by Linnaeus.

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11. The *Oliva* of Montfort, 1808.

In his *Conchyliologie Systématique*, Denys de Montfort did not describe species, but only genera. For the genus *Oliva*, he chose for type species *Oliva panamensis*.

panamensis (p. 387)

ORIGINAL DESCRIPTION.

Olive de Panama. Oliva panamensis seu *porphyrius.*

Voluta porphyria Linn. sp. 61...etc..

(follows a long list of references, previous illustrations, the names in different languages, and a description).

DISCUSSION. The explicit reference to *porphyria* (L., 1758), the cited illustrations and the description leave no doubt whatsoever on the identity of the species. It is evident that the author himself considered that the two names *porphyria* and *panamensis* apply to the same animal.

STATUS: **Objective junior synonym** of ***porphyria*** (L., 1758).

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12. The *Oliva* of Perry, 1811.

In his *Conchology*, Perry introduced three new names. The five *Oliva* illustrations of Perry are quite stylized and some features are obviously exaggerated. Perry gave no references and did not cite previous illustrations.

porphyracea (Pl. 41)

ORIGINAL DESCRIPTION:

No. 2. OLIVA PORPHYRACEA. *Shell* dark purple and white, having three belts or circles enveloping the body; the *spire* also variegated with dark purple spots; the *mouth* red. From a shell in the Museum of Mr. Latham.

DISCUSSION. The illustration and the description are quite compatible with the Pacific form of *O. miniacea* (Röding, 1798).

STATUS: **subjective junior synonym** of ***miniacea*** (Röding, 1798).

Note. This is *porphyria* (L., 1758) according to WAGNER & ABBOTT (1978), ZEIGLER & PORRECA (1978), PETUCH & SARGENT (1986).

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leveriana (Pl. 41)

ORIGINAL DESCRIPTION:

No. 3. OLIVA LEVERIANA. *Shell* of a pale purple and gray, richly studded and adorned with a close net pattern, inclosing the whole body; the *columella* covered with small branched flutings of a white colour, the general colour of the pattern a reddish pink, formed into angular marks. From a shell formerly in the Museum of the late Sir Ashton Lever, in honour of whose zeal for the promotion of natural history and the sciences, I have taken this opportunity of naming it.

DISCUSSION. The drawing and the description leave no doubt that this is *porphyria* (L., 1758).

STATUS: **subjective junior synonym** of ***porphyria*** (L., 1758).

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subviridis (Pl. 41)

ORIGINAL DESCRIPTION:

No. 5. OLIVA SUBVIRIDIS. *Shell* of an olive green, interspersed with curious marks of dark brown, placed in the form of belts; the *mouth* gray, the girdle at the base of a rich brown colour. From a shell in the collection of Mr. Jennings of Chelsea, and supposed to be a native of the southern hemisphere.

DISCUSSION. By a stretch of imagination, one could interpret the description and the rather

caricatural figure as depicting a specimen of either *elegans* Lamarck, 1811, *reticulata* (Röding, 1798) or even *tricolor* Lamarck, 1811.

STATUS: **nomen dubium.**

Note. This is a color form of *tricolor* Lamarck, 1811 according to PETUCH & SARGENT (1986)

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zigzag (Pl. 41)

ORIGINAL DESCRIPTION.

No. 4. OLIVA ZIGZAG. *Shell* pale yellow, thickly interspersed with brownish lines in an irregular and waving pattern, from whence its name; the *mouth* and girdle at the base of a strong orange colour. A native of Ceylon.

DISCUSSION. The drawing and the description leave no doubt that this is *reticulata* (Röding, 1798).

STATUS: **subjective junior synonym** of *reticulata* (Röding, 1798).

Note. This is:

- a variety of *sanguinolenta* Lamarck, 1811 for DAUTZENBERG (1927).
- a color form of *reticulata* (Röding, 1798) according to WAGNER & ABBOTT (1978), ZEIGLER & PORRECA (1969), PETUCH & SARGENT (1986).

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Acknowledgements.

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Index to the names.

valid names are in **bold**.

hepatica (Röding, 1798): nomen nudum.
incrassata (Lightfoot, 1786): valid.
"*O intertincta* Röding, 1798" (in Wagner & Abbott, 1978): not of Röding.
isabella (Röding, 1798): nomen nudum.
ispida (Röding, 1798): nomen dubium.
ispidula (L., 1758): not an *Oliva*.
ispidula (Abel, 1787): non binominal.
ispidula (Born, 1778): junior homonym of *ispidula* (L., 1758).
ispidula (Schröter, 1782): junior homonym of *ispidula* (L., 1758).
ispidula (Gmelin, 1791): junior homonym of *ispidula* (L., 1758).
ispidula Fischer, 1807: junior homonym of *ispidula* (L., 1758).
labradoriensis (Röding, 1798): nomen dubium.
"*leucophaea* Gmelin" (in Mörch, 1850): not of Gmelin.
leveriana Perry, 1811: subjective junior synonym of *porphyria* (L., 1758).
litterata (Röding, 1798): nomen dubium.
maculata (Solander in Dillwyn, 1817): manuscript name.
mauritana (Abel, 1789): non binominal.
mica (Röding, 1798): nomen dubium.
miniacea (Röding, 1798): valid.
miniata (Link,1807): objective junior synonym of *miniacea* (Röding, 1798).
nigrita (Karsten, 1789): valid.
oculata (Röding, 1798): nomen nudum.
oliva (L., 1758): valid.
olivacea (Karsten, 1789): valid.
ornata (Röding, 1798): nomen nudum.
paleacea (Röding, 1798): nomen nudum.
panamensis Montfort, 1808: objective junior synonym of *porphyria* (L., 1758).
papyracea (Röding, 1798): nomen nudum.
plicata Fischer, 1807: nomen dubium.
porphyracea Perry, 1811: subj. junior syn. of *O. miniacea* (Röding, 1798)
porphyria (L., 1758): valid.
porphyrea (Abel, 1789): non binominal.
punctata (Röding, 1798): nomen nudum.
quercina (Röding, 1798): nomen nudum.
reticulata (Abel, 1789): non binominal.
reticulata (Röding, 1798): valid.
ruffina (Gmelin, 1791): not an *Oliva*.
ruffina (Röding, 1798): nomen nudum.
sepultura principis (Abel, 1789): non binominal.
sepultura principis (Röding, 1798): nomen dubium.
sericea (Röding, 1798): valid.
spicata (Röding, 1798): valid.
subviridis Perry, 1811: nomen dubium.
taeniata (Link, 1807): objective junior synonym of *ispida* (Röding, 1798).
tentorium (Link, 1807): objective junior synonym of *porphyria* (L., 1758).
tessellata Lamarck, 1811: objective junior synonym of *olivacea* (Karsten, 1789).
textilis (Röding, 1798): nomen nudum.
tigris (Röding, 1798): nomen nudum.
tuberosa (Röding, 1798): subjective junior synonym of *bulbosa* (Röding, 1798).
tumida (Röding, 1798): nomen nudum.
turgida (Röding, 1798): nomen nudum.
umbrosa (Röding, 1798): nomen dubium.
undulata (Röding, 1798): nomen nudum.
variabilis (Röding, 1798): nomen nudum.
variegata (Röding, 1798): nomen dubium.
ventricosa (Solander in Dillwyn, 1817): manuscript name.
vellus aureum (Abel, 1789): non binominal.
vellus-aureum (Röding, 1798): nomen dubium.
vidua (Röding, 1798): objective junior synonym of *nigrita* (Karsten, 1789).
ziczac (Röding, 1798): nomen nudum.
zigzag Perry, 1811: subjective junior synonym of *reticulata* (Röding, 1798).

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The references to the figures are *verbatim* those used by the authors of the descriptions.

ADANSON

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ARGENVILLE, d'

t. 16. f. K: *porphyria* (Linnaeus, 1758).
t. 16. f. R: *oliva* (Linnaeus, 1758).

GUALTIERI

t. 23. f B: *oliva* (Linnaeus, 1758).
t. 24. f. O: *porphyria* (Linnaeus, 1758).
t. 24. f. P: *porphyria* (Linnaeus, 1758).

KAEMMERER

t. 3. fig. 7: *tuberosa* (Röding, 1798).
t. 3. fig. 8: *tuberosa* (Röding, 1798).

KNORR

1. t. 15. f. 7: *umbrosa* (Röding, 1798).
2. t. 10. f 6: *amethystina* (Röding, 1798)
2. t. 10. f 7: *amethystina* (Röding, 1798).
3. t. 17. f. 3: *fasciata* (Röding, 1798).
3. t. 19. f. 3: *ispida* (Röding, 1798).
5. t. 19. f. 1: *sepultura principis* γ (Röding, 1798).
5. tab. 26. fig. 4: *quercina* (Röding, 1798).
5. t 26. f. 4: *sepultura principis* β (Röding, 1798).
5. t. 27. fig. 5: *quercina* ß (Röding, 1798).
5. t. 28. f. 6: *fusca* (Fischer, 1807).
6. t. 34. f. 4: *dealbata* (Röding, 1798).
6. t. 34. f. 5: *dealbata* (Röding, 1798).

LISTER

4. f. 10. c. 1. t. 2: *oliva* (Linnaeus, 1758) (not seen)
t. 664. f. 8: *crassa* (Gmelin, 1791).
720. 6: *porphyria* (Linnaeus, 1758).
731. f. 20: *annulata* (Gmelin, 1791)
t. 746. f. 40: *tumida* (Röding, 1798).

MARTINI

tab. 45. fig. 472: *nigrita* (Karsten, 1789).
2. t. 45. f. 472: *fusca* (Fischer, 1807).
2. t. 45. f. 472: *vidua* (Röding, 1798).
tab. 45. fig. 473: *nigrita* (Karsten, 1789).
2. t. 45. f. 473: *vidua* (Röding, 1798).
2. t. 45. f. 473: *fusca* (Fischer, 1807).
2. t. 45. f. 476: *miniata* (Link 1807).
2. t. 45. f. 476: *miniacea* (Röding, 1798).
2. t. 45. f. 477: *miniata* (Link, 1807).
2. t. 45. f. 477: *miniacea* (Röding, 1798).
2. t. 45. f. 478: *variegata* (Röding, 1798).
2. t. 45. f. 479: *variegata* (Röding, 1798).
2. t. 45. f. 480: *variegata* α (Röding, 1798).
2. t. 45. f. 480: *sepultura principis* γ (Röding, 1798).
2. t. 45. f. 481: *variegata* α (Röding, 1798).
2. t. 45. f. 481: *sepultura principis* γ (Röding, 1798).
2. t. 46. f. 485: *tentorium* (Link, 1807).
2. t. 46. f. 486: *tentorium* (Link, 1807).
2. t. 46. f 488: *litterata* (Röding, 1798).
2. t. 46. f. 490: *vellus-aureum* (Röding, 1798).
2. t. 46. f. 491: *amethystina* (Röding, 1798).
2. t. 46. f. 491: *aurata* (Link, 1807).
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T. 2. tab. 46. fig. 494: *olivacea* (Karsten, 1789).
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Vol. II- f. 500: *incrassata* (Lightfoot, 1786).
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2. t 48. f. 509: *arachnoidea* (Röding, 1798).
2 t. 48. f. 510: *spicata* (Röding, 1798).
2. t 48. f. 510: *arachnoidea* (Röding, 1798).
2. t 48. f. 512: *reticulata* (Röding, 1798).
2. t. 48. f. 515: *coerulea* (Link, 1807).
2. t. 48. f. 516: *coerulea* (Link, 1807).
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2. t. 49. f. 522: *ispida* β (Röding, 1798).
2. t. 49. f. 523: *ispida* β (Röding, 1798).
2. t. 49. f. 524: *ispida* (Röding, 1798).
2. t. 49. f. 525: *ispida* (Röding, 1798).
2. t. 49 f. 527: *mica* var α (Röding, 1798).
2. t. 49 f. 528: *mica* var α (Röding, 1798).
2. t. 49 f. 529: *mica* var α (Röding, 1798).

2. t. 49. f. 530: *ispida* (Röding, 1798).
2. t. 49. f. 530: *taeniata* (Link, 1807).
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2. t. 51. f. 561: *sericea* (Röding, 1798).
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PETIVER. Gazophil.,1767.
t. 59. f. 8: *ispidula* (Linnaeus, 1758).

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t. 39. f. 4: *oliva* (Linnaeus, 1758).
t. 39. f. 4: *sepultura principis* (Röding, 1798).
t. 39. f. 5: *oliva* (Linnaeus, 1758).
t. 39. f. 5: *caerulea* (Röding, 1798).
t. 39. f. 6: *ispidula* (Linnaeus, 1758).
t. 39. f. 7: *ispidula* (Linnaeus, 1758).

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Contribution to the knowledge of the family Caecidae. 1. A new *Caecum* from Canary Islands (Caenogastropoda: Rissooidea) *

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ABSTRACT. A very peculiar, new species of the meiobenthic gastropod family Caecidae is described and figured from the Canary Islands: *Caecum lightfootae* n.sp. It is compared with all the known congeneric species from this area.

KEYWORDS: *Caecum*, new species, meiobenthic, North-East Atlantic, Recent, marine.

INTRODUCTION

The Caecidae are a worldwide distributed family of rissooidean gastropods with secondary uncoiled teleoconch, adapted to the meiobenthic life. Despite a good deal of efforts, past and recents, to the study of their taxonomy (see i.e. De Folin 1867-1876, 1867, 1875, 1880; Carpenter 1858-1859; Moore 1962; Van Aartsen 1977; Lightfoot 1992a, b, c, 1993a, b), Caecidae are still one of the less-known prosobranch family. The use of classical morphology in their taxonomy is often hampered by the difficulty in individuating good characters in their simple, unusual tube-like shells. Even worse is the situation as for their supraspecific classification. Anatomical data-sets are still poor and insufficient to create a good phylogenetic scheme of the family.

A revision of the North-East Atlantic members of the family, presently in progress by the authors, is revealing some important novelties as for their taxonomy. Preliminary to this revision, some still undescribed species need to be presented.

Working on some samples from the Canary Islands, a very peculiar species of *Caecum* was sorted out. It is a new species, different from all the other species known from that area.

SYSTEMATICS

Superfamily RISSOOIDEA Gray J.E., 1847
Family CAECIDAE Gray M.E., 1850
Genus *Caecum* Fleming, 1813

Caecum lightfootae n. sp.

DESCRIPTION (holotype's measurements between parentheses)

Teleoconch uncoiled, tube-like. Shell very small for the genus, semitransparent, glossy. Tube very curved, regularly bent, slightly subconical for one third of the length (on the septum side), then nearly cylindrical for the rest (Figs. 1, 2). Surface seemingly smooth, with a microsculpture of only thin and irregular growth lines. Aperture regularly circular, with a more or less pronounced varix, always present (Fig. 3). Septum not retracted, with the lateral outline subtriangular and blunt. Mucro protruding, and right-handed when observed frontally (Figs. 4, 5). Protoconch and growth stages not identified amidst the available material. Shell whitish, with irregular

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wax-vitreous areas. Operculum thin, corneous, yellow-brownish; external surface with 4-5 concentrical ridges, the central and the outer part smooth. Soft parts not studied at present. Dimensions: lenght 1.15-1.30 mm (1.23); tube diameter at the septum level 0.24-0.26 mm (0.25); tube diameter at the aperture 0.34-0.36 mm (0.35).

Material examined: Punta Blanca, Puerto Santiago (Is. Tenerife, Canary Islands) - 30 m, M.Oliverio leg. 12-IX-1992: 28 shells. Arigana (Is. Gran Canaria, Canary Islands) - 1 m, F.Gubbioli leg.: 1 specimen.

The type material, all from the type locality, has the following location:

Holotype and one paratype Museo Civico di Zoologia, Roma

2 paratypes Laboratorio di Malacologia, Università di Bologna

2 paratypes Muséum National d'Histoire Naturelle, Paris

2 paratypes Natural History Museum, London

2 paratypes Florida Museum Natural History, Gainsville

2 paratypes Australian Museum, Sydney

2 paratypes Swedish Museum of Natural History, Stockholm

2 paratypes Museo Insular Ciencias Naturales, Sta Cruz de Tenerife

Other paratypes are stored in the private collection of M. Pizzini (2), I. Nofroni (2), M. Oliverio (2), C. Schander (2), L. Tringali (2), G. Ambrosiano (1), F. Gubbioli (1).

Type locality. Punta Blanca, Puerto Santiago, Is. Tenerife, Canary Islands (Spain). At present the species is known only from Canary Islands, Is. Tenerife and Is. Gran Canaria.

Etymology. The species is dedicated to a very keen american malacologist: the late Mrs. Joanne Lightfoot, known to the specialists of this family for her studies on the Caecidae of North America. The first author had the possibility to appreciate her scientific and human endowments, during a short but intense mail correspondence.

Discussion. Although the morphological features of *C. lightfootae* are so peculiar to render it unic and easily separable from any other Canaric Caecidae, we prefer to compare it with all the other species known from this area.

NORDSIECK & TALAVERA (1979: 84) recorded only five *Caecum* species from the Canary Islands: *C. atlantidis* Watson, 1897, *C. trachea* (Montagu, 1805), *C. glabrum* (Montagu, 1803), *C. vitreum* Carpenter, 1858 and *C. elegantissimum* Carpenter, 1858. Evidently, they skipped *C. clarkii* Carpenter, 1858, though its type locality was just Is. Tenerife. To this list a seventh species should be added, namely *C. armoricum* DE FOLIN, 1869 recently recorded by HOEKSEMA & SEGERS (1993: 86) for the Canary Islands (Gran Canaria).

C. lightfootae has a septum similar to that of *C. clarkii* and *C.vitreum*. It differs by its smaller size, by the lack of a longitudinal sculpture more (*clarkii*) or less (*vitreum*) evident, by the presence of the annular varix at the aperture, and finally by its pronounced curvature.

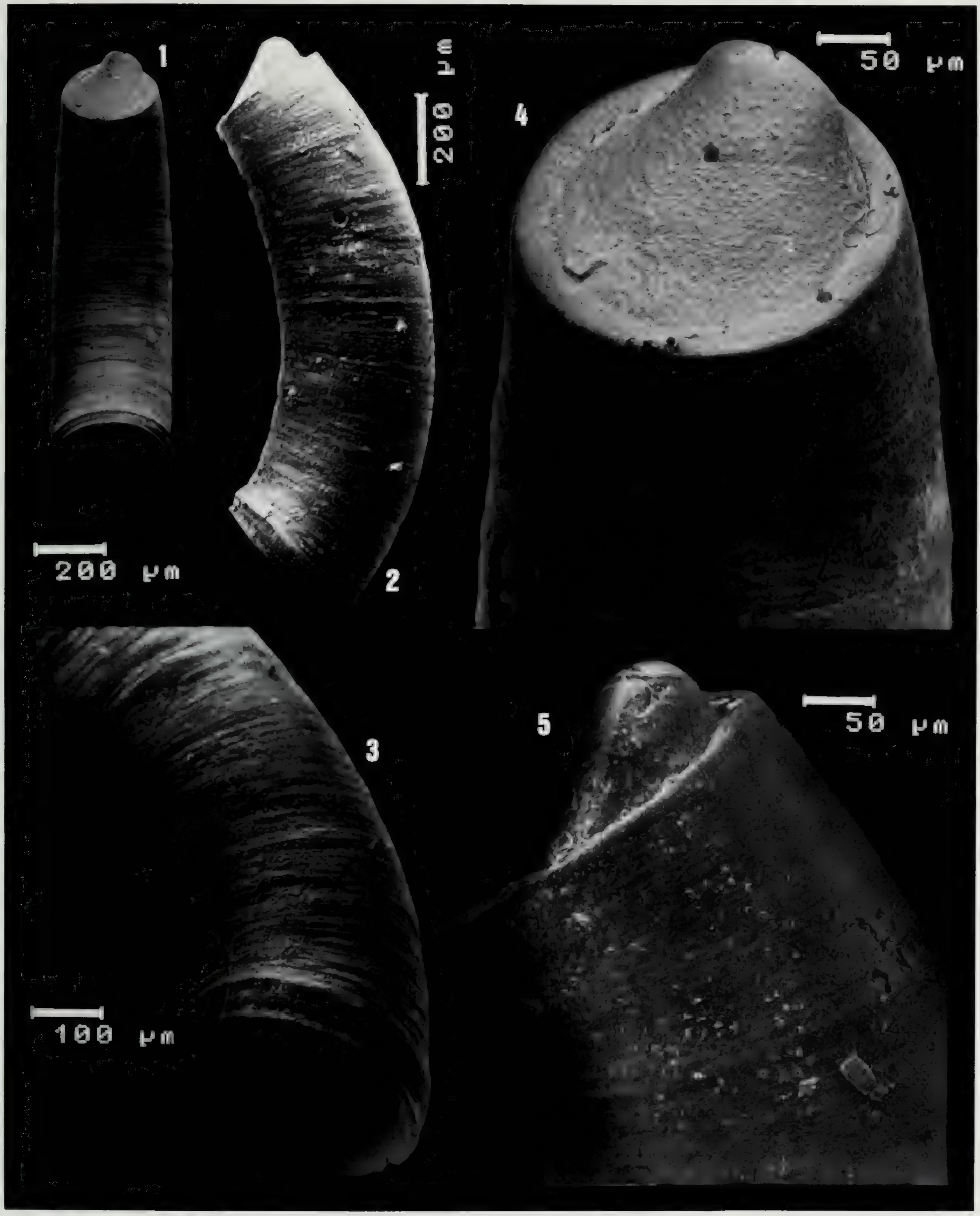
C. glabrum and *C. armoricum* are easily separable from the new species by a different septum (dome-shaped in the first, and nail-shaped in the second), and by their lack of an apertural varix.

C. atlantidis, *C. trachea* and *C. elegantissimum* are completely different and unrelated species, with an evident annular sculpture, completely absent in *C. lightfootae*.

A further european species, namely *C. auriculatum* De Folin, 1868 (whose type series we have studied), needs a brief comparison, although it is not recorded for the Canary Islands. Its septum is nearly hemispheric, with a mucro hear-like, usually right-handed; the colour is uniformly white vitreous. Finally, *C. auriculatum* is more curved, has a larger mean size, and the apertural varix is more evident than in *C. lightfootae*.

Acknowledgements. We are grateful to Dr. Christoffer Schander (University of Göteborg, Sweden) for the numerous (too much!) SEM pictures he realized for us.

Figs. 1-5 (opposite).
Caecum lightfootae n.sp. holotype. Is. Tenerife.
1. General view (frontal).
2. General view (lateral).
3. Aperture.
4. Apex (frontal view).
5. Apex (lateral view).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2
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3
100 µm
5
50 µm

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Révision des Muricidae de l'Eocène de la falaise de la Côte des Basques à Biarritz (Pyrénées-Atlantiques, France)

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RESUME: Cinq espèces de l'Eocène supérieur de Biarritz (Priabonien de la Côte des Basques, Les Bains) sont décrites. Deux sont nouvelles: *Siphonochelus (Laevityphis) biarritzensis* et *S. (Trubatsa) evainae*. *Pterynotus (Pterynotus)* cf. *consobrinus* (d'Orbigny, 1852), du Stampien de Gaas (Landes) est cité pour la première fois dans le Priabonien de Biarritz. *Murex (Pteronotus) subfiligrana* Tournouër *in* de Bouillé, 1876 est révisé.

ABSTRACT: Five species from the Priabonian of Biarritz (Côte des Basques, Les Bains, Pyrénées-Atlantiques, France) are described. Two species are new: *Siphonochelus (Laevityphis) biarritzensis* and *S. (Trubatsa) evainae*. *Pterynotus (Pterynotus)* cf. *consobrinus* (d'Orbigny, 1852) is recorded for the first time in the Priabonian of Biarritz. Previously, the species was only known in the Stampian of Gaas (Aquitaine basin). *Murex (Pteronotus) subfiligrana* Tournouër *in* de Bouillé, 1876 is revised.

MOTS-CLES: Muricidae, Eocène supérieur, Priabonien, Bassin d'Aquitaine, systématique, phylogénie.

KEY-WORDS: Muricidae, Upper Eocene, Priabonian, Aquitaine Basin, systematics, phylogeny.

INTRODUCTION

Les Muricidae de l'Eocène de la Côte des Basques (Biarritz) sont connus par deux espèces citées par Tournouër *in* de Bouillé (1876) qui proviennent des Marnes des Bains. A la suite de recherches à l'Université de Bordeaux I, j'ai retrouvé plusieurs Muricidae provenant de cette localité dans la collection Neuville. Cette découverte m'a incité à rechercher dans d'autres collections des Muricidae de l'Eocène de la Côte des Basques. Les collections Castex (Muséum d'Histoire naturelle de Biarritz), Cossmann (Muséum national d'Histoire naturelle de Paris - Laboratoire de Paléontologie) et Tournouër (Institut de Géologie A. de Lapparent) ont livré d'autres exemplaires de cette famille.

L'ensemble rassemblé constitue peu d'individus, mais complète nos connaissances sur les Muricidae de l'Eocène supérieur d'Aquitaine.

Situation géographique de la Côte des Basques (Les Bains): Carte géologique 1/50.000, feuille XII-44 (Bayonne); x = 284.125, y = 3138.300.

Cadre stratigraphique: Le Paléogène des falaises de Biarritz a été révisé par Mathelin (1988). Mathelin situe les Marnes des Bains, épaisses de 350 m, au-dessus des Marnes à *Turbinolia calcar* (=*Flabellum calcar*). D'après le nannoplancton calcaire, il place les Marnes des Bains dans les biozones NP19 (*Isthmolithus radians*) et NP20 (*Sphenolithus pararadians*), définies par MARTINI (1971). STEURBAUT (in NOLF, 1988) place également les Marnes des Bains dans NP 20. Ces deux biozones permettent de dater le Priabonien terminal.

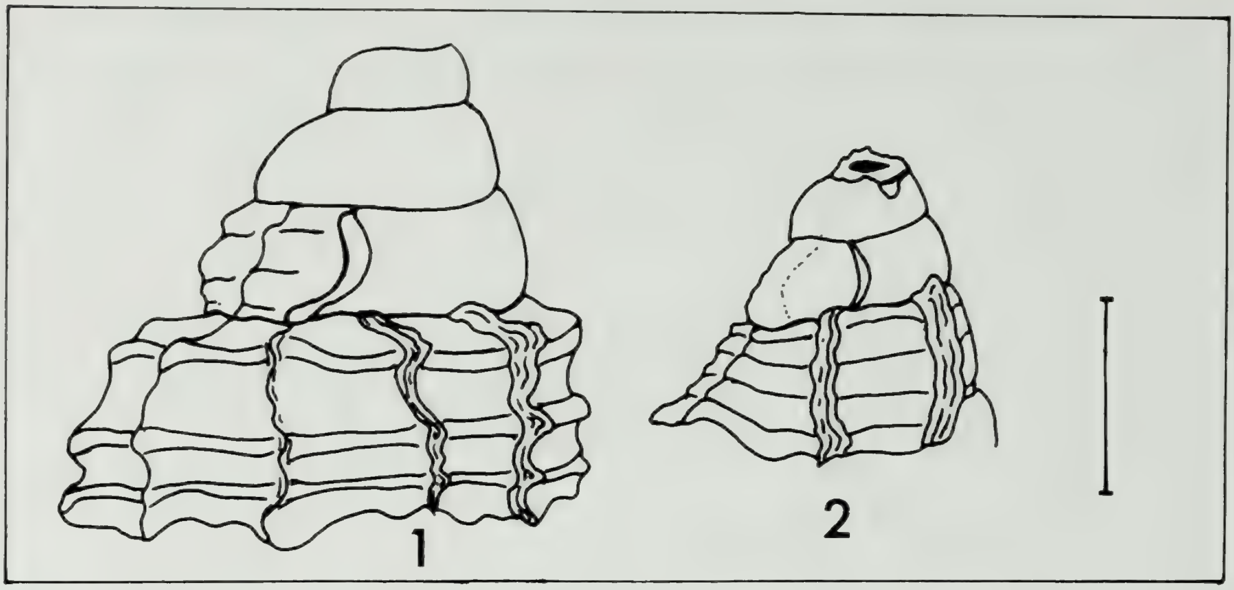
Abréviations utilisées:

Collections:

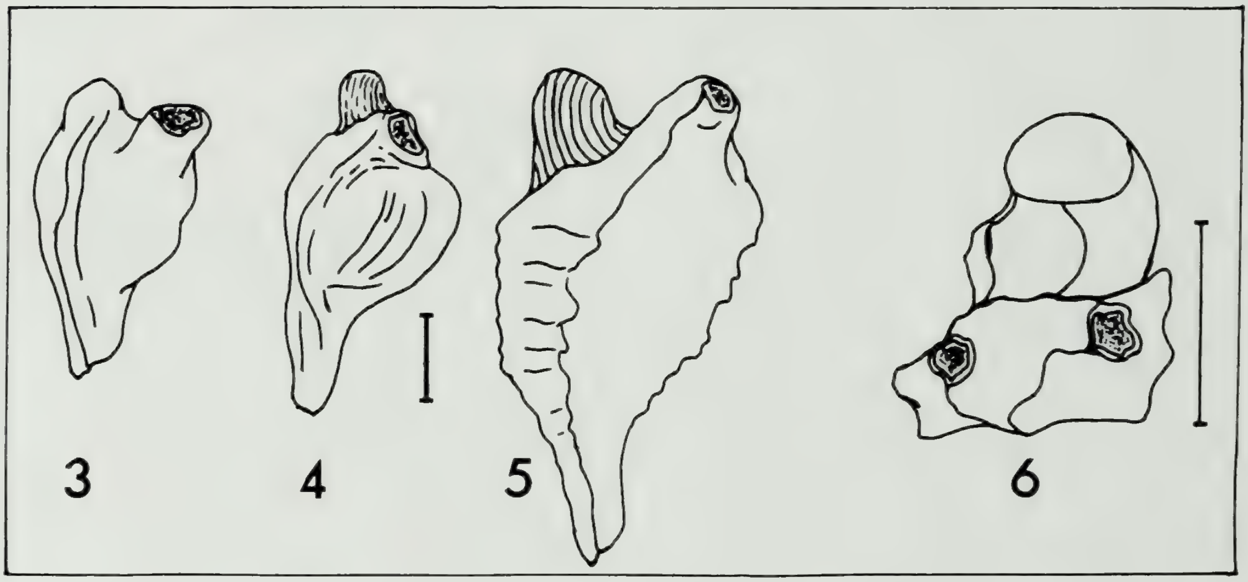
UBX: Université Bordeaux I, Talence; MNHN-LP: Muséum national d'Histoire naturelle de Paris (Laboratoire de Paléontologie); BIA: Muséum d'Histoire naturelle de Biarritz; IGAL: Institut de Géologie A. de Lapparent, Cergy.

Mensurations:

H: hauteur; D: diamètre; HO: hauteur de l'ouverture; LO: largeur de l'ouverture; G: chez les Typhinae, angle du tube par rapport à l'axe (selon Houart, 1991).



Figures 1-2 (échelle: 1 mm)
1. Protoconque de *Chicoreus (?) subfiligrana* (Tournouër *in* de Bouillé, 1876), néotype, collection Neuville (UBX, n°TYFIPAL 57.2.1).
2. Protoconque de *Pterynotus (Pterynotus) crenulatus* (Röding, 1798), collection Neuville (UBX, n°TYFIPAL 57.2.2).



Figures 3-6 (échelle: 1 mm)
3. Profil de l'ouverture et dernière côte de *Siphonochelus (Laevityphis) biarritzensis* nov sp, paratype, collection Cossmann (MNHN LP n°J00003).
4. Profil de l'ouverture et dernière côte de *S. (Trubatsa) evainae* nov. sp., paratype, collection Castex (BIA).
5. Profil de l'ouverture et dernière côte de *S. (T.) gaasensis* (d'Orbigny, 1852), collection Merle (localité: Gaas).
6. Protoconque de *S. (L.) biarritzensis* nov sp, holotype, collection Neuville (UBX, n° TYFIPAL 57.2.3)

ETUDE SYSTEMATIQUE

Famille MURICIDAE Rafinesque, 1815
Sous-famille MURICINAE Rafinesque, 1815
Genre *Chicoreus* Montfort, 1810
Espece-type: *Murex ramosus* Linné, 1758 par désignation originale.

Chicoreus (?) subfiligrana
(Tournouër *in* de Bouillé, 1876)
(Figs. 1, 7, 8)

Murex (Pteronotus) subfiligrana Tournouër *in* de Bouillé, 1876: p. 58, pl.III, fig.7. Localité-type: Biarritz (Côte des Basques, Les Bains).

Niveau-type: Marnes à *Turbinolia calcar*, Priabonien de Biarritz.

Materiel-type: Je n'ai pas retrouvé l'holotype dans la collection Tournouër déposée à l'IGAL, où il existe des fossiles de la Côte des Basques. L'holotype a le labre cassé et ne présente que les quatre derniers tours. D'après Tournouër, sa hauteur est de 35 mm et son diamètre de 18 mm. Un spécimen à spire complète, mais avec le canal siphonal et l'ouverture cassés a été retrouvé dans la collection Neuville (UBX, n°TYFIPAL 57.2.1). Il est désigné ici comme néotype.

Autre matériel: 1 fragment de labre, collection Cossmann n° 16453a (MNHN-LP n°J00001).

Description: Coquille d'environ 30 mm de hauteur (hauteur estimée) et de 15 mm de diamètre. Protoconque conique composée de 3,5 tours. Téléoconque composée de 6 tours étagés. Sculpture axiale composée de 3 côtes principales subépineuses dans l'intervalle desquelles s'intercale une côte intermédiaire. Sculpture spirale composée de 3 à 4 cordons spiraux sur la spire et de 10 cordons sur le dernier tour. Microsculpture formée de fins cordonnets spiraux croisés par les stries d'accroissement grossières, l'ensemble donnant l'aspect d'une surface écailleuse. Bord columellaire lisse. Labre droit, liré. Canal siphonal court (d'après la figure de l'holotype).

Dimensions: Néotype, H: 15 mm (base incomplète); D: 11 mm (ouverture incomplète).

Comparaisons: TOURNOUER *in* DE BOUILLE, 1876 compare ce Muricidae à *Murex filigrana* von Koenen, 1867, du Lattorfien d'Allemagne. Cette comparaison se justifie par une microsculpture développée et une symétrie à trois côtes principales. Toutefois, les côtes principales de *M. filigrana* sont plus développées et plus foliacées. Ses cordons spiraux sont plus fins et son ouverture porte deux cals sur le bas de la columelle. Enfin, les anciens canaux siphonaux sont nettement abaxiaux alors que ceux du *M. subfiligrana* sont droits. Les caractères de *M. filigrana* rapellent ceux des *Pterynotus* actuels de l'Océan Pacifique tels que *P. (P.) pellucida* (Reeve, 1845) ou *P. (P.) tripterus* (Born, 1778). A l'instar de Tournouër, je considère les *M. filigrana* et *M. (P.) subfiligrana* comme deux epèces distinctes.

Discussion sur la position générique:. Les caractères du *Murex subfiligrana* (symétrie à trois côtes principales, côtes subépineuses, présence d'une microsculpture et bord columellaire lisse, voir HOUART, 1992) permettent un rapprochement avec *Chicoreus* Montfort, 1810. D'après HOUART (1992), *Chicoreus (Chicoreus)* se distingue *C. (Triplex)* par la présence de dent labiale. Le mauvais état de l'ouverture de notre échantillon le plus complet empêche de faire cette distinction. *C. (T.) tateiwai* Hatai & Kotaka, 1952 , du Miocène inférieur de Corée, ressemble à l'espèce de Biarritz, mais sa microsculpture est moins développée.

Murex subfiligrana ne peut se classer dans *Phyllonotus* Swainson 1833 (que VOKES (1990) admet comme sous-genre de *Chicoreus*), qui présente souvent une spire plus basse, une sculpture spirale plus grossière et fréquemment plusieurs cals ou une série de rides columellaires. *C. (Phyllonotus) initialis* Vokes, 1990, de l'Eocène moyen du Texas possède des côtes principales plus foliacées avec deux côtes intermédiaires, et se remarque par ses cordons spiraux plus épais.

Genre *Pterynotus* Swainson, 1833
Espece-type: *Murex pinnatus* Swainson, 1822 par désignation originale.
Sous-genre *Pterynotus* Swainson, 1833

Pterynotus (Pterynotus) crenulatus (s.l.)
(Röding, 1798)
(Figs. 2, 9)

Purpura crenulata Röding, 1798: Museum Boltenianum: 144 (d'après Brander, 1766, pl.3, figs 77, 79).

Synonymie: *Murex tricarinatus* Lamarck, 1803: Ann. Mus. natn. Hist. nat. Paris, v.II : 223. *Murex (Pteropurpura) palensis* Magne, 1940: J. de Conch., v. 84: 372.

Réference concernant Biarritz: *Murex trigonus* -Tournouër *in* de Bouillé, 1876: 50; non Rouault, 1850: 493 , pl.XVII, fig.17.

Materiel examiné: 1 spécimen, collection Neuville (UBX, N°TYFIPAL 57.2.2); 1 spécimen cassé au niveau du labre, collection Cossmann n° 16978 (MNHN-LP).

Description: Coquille trapue de 9 mm de hauteur et de 5 mm de diamètre. Protoconque conique, multispirale dont 2,5 tours sont conservés, le sommet étant cassé. Téléoconque composée de cinq tours. Côtes foliacées non épineuses au sommet. Présence d'une côte intermédiaire entre les côtes foliacées. Quatre cordons sur la spire et 18 cordons sur le dernier tour. Ouverture subcirculaire à bord columellaire distinct. Sept dents internes. Canal siphonal court, légèrement orienté à gauche.

Dimensions: H: 9,5 mm; D: 5,6 mm; H/D: 1,71; HO: 5,3 mm; LO: 2,8 mm; HO/LO: 1,89.

Considérations nomenclaturales sur l'espèce: En accord avec VOKES (1971), LE RENARD (1992) considère *Murex tricarinatus* Lamarck, 1803 comme un synonyme postérieur de *Purpura crenulata* Röding, 1798. MERLE (1990) admet pour l'espèce *tricarinatus* quatre transiants. Ceci m'amène à proposer les combinaisons nomenclaturales suivantes:

1°) *Pterynotus (P.) crenulatus trigonus* (Rouault, 1850) pour *Murex trigonus* Rouault, 1850 du Cuisien du Béarn.

2°) *P. (P.) crenulatus crenulatus* (Röding, 1798) du Lutétien anglo-franco-belge.

3°) *P. (P.) crenulatus tricuspidatus* (Deshayes, 1865) pour *Murex tricuspidatus* Deshayes, 1865, du Lutétien supérieur anglais, de l'Auversien du Bassin de Paris et du Bartonien anglais.

4°) *P. (P.) crenulatus brevicauda* (Hébert, 1849) pour *Murex brevicauda* Hébert, 1849, du Lattorfien et de l'Oligocène d'Allemagne.

Comparaisons avec des populations conspécifiques: Les deux spécimens, dont celui de la collection Neuville est cité par MAGNE (1940, p.372), sont très comparables aux jeunes individus de *P. (P.) crenulatus trigonus*, de l'Eocène du Béarn. A la différence des spécimens de Gan qui portent 2 à 3 côtes intermédiaires entre les côtes foliacées, ceux de Biarritz n'en portent qu'une seule. De plus, le sommet des côtes foliacées n'est pas épineux. Ce caractère les distingue de *P. (P.) crenulatus crenulatus* et de *P. (P.) crenulatus tricuspidatus*. En revanche, il les rapproche de *P. (P.) crenulatus brevicauda* du Lattorfien.

Comme il s'agit de formes juvéniles, ce rapprochement avec *P. (P.) crenulatus brevicauda* ne peut être certain. En revanche, l'attribution à l'espèce *crenulatus* ne fait pas de doute.

Pterynotus (P.) cf. *consobrinus*

(d'Orbigny, 1852)
(Figs. 10, 11)

Murex consobrinus d'Orbigny, 1852: Prodr., t. III, n°1346.

Autres références: *Murex (Pteropurpura) consobrinus* - MAGNE, 1940: J. de Conch., v.84: 370-376, pl. II, fig. 3, 4.

Localité-type: Gaas (Landes).

Etage-type: Holotype, Université de Bordeaux I.

Matériel de Biarritz. 1 spécimen incomplet, collection Cossmann n°16453 a (MNHN-LP n°J00002); 1 spécimen très jeune de 2 mm de hauteur, collection Tournouër (IGAL).

Description: Coquille à spire élancée. Protoconque lisse, paucispirale composée de 1,5 tour. Côtes foliacées assez planes et non épineuses sur la spire. Une côte intermédiaire bien marquée entre les côtes foliacées. Deux cordons spiraux sur la spire et cinq visibles jusqu'à la partie pariétale du dernier tour.

Dimensions: H (jusqu'à la partie pariétale): 12 mm; D: 9 mm.

Comparaisons: Cette espèce ne peut être confondue avec le *P. (P.) crenulatus* de Biarritz, plus trapu, dont les côtes principales sont plus fortes et dont les cordons spiraux sont plus nombreux (4 sur la spire au lieu de 2).

Je compare ces deux spécimens à deux petits spécimens de *P. (P.) consobrinus* de Gaas provenant de ma collection. La sculpture est analogue puisqu'elle est formée de deux cordons spiraux sur la spire et d'une côte intermédiaire bien marquée (Fig.12). D'autre part, la protoconque lisse et paucispirale est analogue chez les spécimens de Biarritz et de Gaas. Pour ces raisons, je rapproche les individus de Biarritz de *P. (P.) consobrinus*, mais la mauvaise qualité du matériel m'empêche d'en être totalement certain.

Sous-famille TYPHINAE Cossmann, 1903
Genre *Siphonochelus* Jousseaume, 1880
Sous-genre *Laevityphis* Cossmann, 1903
Espèce-type: *Typhis coronarius* Deshayes , 1865 (=*Typhis muticus* J. Sowerby, 1834) par désignation originale.

Siphonochelus (Laevityphis) biarritzensis nov. sp.
(Figs. .3, 13, 14, 15, 16)

Matériel-type: Holotype, collection Neuville (UBX, n°TYFIPAL 57.2.3); paratype, collection Cossmann (MMNHN-LP n°J00003).
Localité-type: Biarritz (Les Bains).
Niveau-type: Marnes à Turbinolia calcar (Priabonien de Biarritz).
Etymologie: *biarritzensis*: de Biarritz.
Dimensions de l'holotype: H: 6,2 mm; D: 3,2 mm; HO: 1,4 mm; LO: 0,9 mm; G: 55°.
Dimensions du paratype: H: 8,6 mm; D: 3,8 mm; HO: 1,8 mm; LO: 1,1 mm. G: 30°
Diagnose: Petite coquille de 6 mm à 8 mm de hauteur et de 3,5 mm à 3,8 mm de diamètre. Protoconque paucispirale et globuleuse composée de 3/4 de tour. Téléoconque composée de quatre tours étagés. Dernier tour égal à la moitié de la hauteur totale. Suture bien visible et profonde. Sculpture spirale obsolète sur le dernier tour. Scupture axiale composée de quatre stades de développement par tour comprenant chacun une côte large dissociée du tube. Côtes lisses. Tubes s'écartant de l'axe de 37° en moyenne. Ouverture subcirculaire à péristome marqué. Canal siphonal clos, court.

Comparaisons: *Siphonochelus (L.) muticus*, du Cuisien du Bassin de Paris se distingue par sa protoconque composée de 3,5 tours. Ses côtes sont aussi nettement plus fines et son ouverture plus ovale. Sa spire est élancée alors que celle de *S. (L.) biarritzensis* est étagée.

Siphonochelus (L.) gracilis (Conrad, 1833), du Claibornien des Etats-Unis (Eocène moyen) présente une morphologie voisine de *S. (L.) muticus* et n'en diffère que par sa spire encore plus élancée. *Murex alternata* Lea, 1833 est synonyme de cette espèce (PALMER, 1937).

Siphonochelus (L.) thagus (Olsson, 1930), de l'Eocène supérieur du Pérou (Talara Formation, Yasila) présente une spire élancée et n'a pas les tours étagés de *S (L.) biarritzensis*. En revanche, ses côtes sont plus épaisses que celles de *S. (L.) muticus* et de *S. (T.) gracilis*.

Position générique. Cette espèce peut se classer dans le sous-genre *S.(Laevityphis)* en raison de sa petite taille et de ses côtes lisses, nettement dissociées des tubes.

Sous-genre *Trubatsa* Dall, 1889
Espèce-type: *Typhis (Trubatsa) longicornis* D'Orbigny, 1850, par désignation originale.

Siphonochelus (Trubatsa) evainae nov. sp.
(Figs. 4, 17, 18, 19, 20))

Matériel: Holotype: collection Neuville (UBX, n°TYFIPAL 57.2.4); paratype n° 67.04.03, collection Castex (BIA); autres spécimens: 2 spm: collection Cossmann (MNHN-LP n°J00004).
Localité-type: Biarritz, Côte des Basques.
Niveau-type: Marnes à *Turbinolia calcar* (Priabonien de Biarritz).
Etymologie: *evainae*: d'Evaine, ma fille nouvelle née.
Dimensions de l'holotype: H: 9,6 mm; D: 5,6 mm; HO: 2,0 mm; LO: 1,3 mm; G: 63°.
Dimensions du paratype: H: 7,4 mm; D: 4,1 mm: HO: 1,7 mm; LO: 1,2 mm. G: 65°.
Dimensions des specimens de la collection Cossmann: H: 7,6 mm, 6,9 mm; D: 3,9 mm, 3,3 mm; HO: 1,7 mm, 1,4 mm; LO: 1,2 mm, 0,9 mm; G: 56°, 53°.
Diagnose: Coquille trapue de 7 à 9 mm de haut et de 4 à 5 mm de diamètre. Protoconque conique, multispirale, composée de 3,5 tours. Téléoconque composée de quatre tours. Dernier tour égal au 2/3 de la hauteur totale. Suture visible. Sculpture spirale ornée de un ou deux cordons obsolètes sur la partie centrale du dernier tour. Sculpture axiale composée de quatre côtes totalement associées aux tubes. Présence d'un cal partant de la base du tube, s'appliquant à la base de la côte du tour précédent et recouvrant une partie de la suture. Tube anal s'écartant de l'axe de 59° en moyenne. Ouverture ovale à péristome marqué. Canal siphonal clos, large.
Comparaisons: Les deux spécimens de la collection Cossmann se trouvaient mélangés avec un spécimen de *S. (Laevityphis) biarritzensis* décrit ci-dessus. L'ensemble avait originellement été identifié comme *Typhis pungens* Solander, puis Cossmann a remplacé, sur l'étiquette, ce nom par celui de *Typhis newtoni*. Dans un autre tube portant

originellement l'étiquette *T. newtoni*, se trouvaient six fossiles de Barton parmi lesquels on peut reconnaître cinq *Typhis (T.) pungens* et un *S. (Trubatsa) parisiensis*. Dans ce tube, Cossmann a écrit :"spire beaucoup plus courte que *T. fistulosus*". Cossmann fait très probablement allusion à *S. (T.) parisiensis* [car *S. (Siphonochelus) fistulosus* (Brocchi, 1814) n'existe pas à Barton]. *T. newtoni* paraît être un nom manuscrit. A mon avis, il désignait plutôt les individus de Barton, que ceux de Biarritz.

Siphonochelus (T.) parisiensis (d'Orbigny, 1850), de l'Eocène d'Europe diffère de *S. (T.) evainae* par sa grande taille (de 16 à 23 mm de hauteur), par sa spire plus élancée, par sa protoconque globuleuse de 1,5 à 2 tours et par ses côtes ne portant pas de cal recouvrant la suture du tour précédent.

Siphonochelus (T.) gaasensis (Tounouër *in* Benoist, 1880), du Stampien d'Aquitaine diffère par sa taille dépassant 26 mm (pour un individu de 5 à 6 tours) et par des sillons spiraux sur la partie externe des côtes. Un cal partant du sommet des côtes et débordant sur la suture est un caractère commun avec *S.(T.) evainae* (fig.5). On ne peut confondre *S. (T.) evainae* avec le jeune de *S. (T.) gaasensis* qui porte déjà des sillons spiraux marqués et dont la spire est bien plus courte.

Siphonochelus (T.) hortensis (Oppenheim, 1900), du Priabonien d'Italie est aussi de grande taille. Il porte comme *S.(T.) gaasensis* des sillons spiraux sur la partie externe des côtes. Le sommet des côtes ne porte pas de cal.

Siphonochelus (T.) nigeriensis Arua, 1981, de l'Ameki Formation (Eocène moyen du Niger), ressemble à *S. (T.) evainae* par sa taille (de 6 à 9,5 mm) et par la présence au sommet des côtes d'un cal débordant sur la suture du tour précédent et par ses côtes dépourvues de crénelures. Il se distingue par sa spire plus étagée, par l'absence de cordons spiraux et par sa protoconque de 1,5 tours.

Considérations phylogénétiques: *Siphonochelus parisiensis, S. hortensis* et *S. gaasensis* semblent constituer une même lignée de *Trubatsa* paléogènes. Elles ont en commun une grande taille (20 à 30 mm), et le port de crénelures sur les côtes. La protoconque, observée chez *S. (T.) parisiensis* est de type paucispiral. L'évolution de *S. (T.) parisiensis* conduit très probablement à *S. (T.) hortensis* au Priabonien. La sculpture spirale développée chez *S. (T.) hortensis* et chez *S. (T.) gaasensis* constitue à mon sens une synapomorphie, témoin d'un ancêtre commun.

Siphonochelus (T.) evainae et *S (T.) nigeriensis*, par leur petite taille (6 à 9 mm) et par l'absence de crénelure sur les côtes, semblent appartenir un groupe différent de celui de *S. (T.) parisiensis*. Le cal porté sur les côtes, qu'on retrouve chez *S. (T.) gaasensis* et chez *S. (T.) nigeriensis* résulterait d'un parallèlisme.

Position générique: L'ensemble de ces espèces porte des côtes totalement associées aux tubes. Pour cette raison, elles sont très voisines de *S. (T.) longicornis,* espèce-type du sous-genre *Trubatsa* Dall, 1889.

Remerciements: Je tiens à exprimer ma gratitude à L. Rousselle et B. Cahuzac de l'Université de Bordeaux I, Talence, à J. Harambillet du Muséum d'Histoire naturelle de Biarritz et à L.Gauthier de l'IGAL, qui m'ont permis d'emprunter les si rares Muricidae récoltés à Biarritz. Mes remerciements vont aussi à R. Houart et à P. Bouchet qui ont relu ce manuscrit. Les clichés photographiques sont de L. Merlette et les clichés au MEB sont de C. Chantograin. La planche photographique a été montée par F. Pilard.

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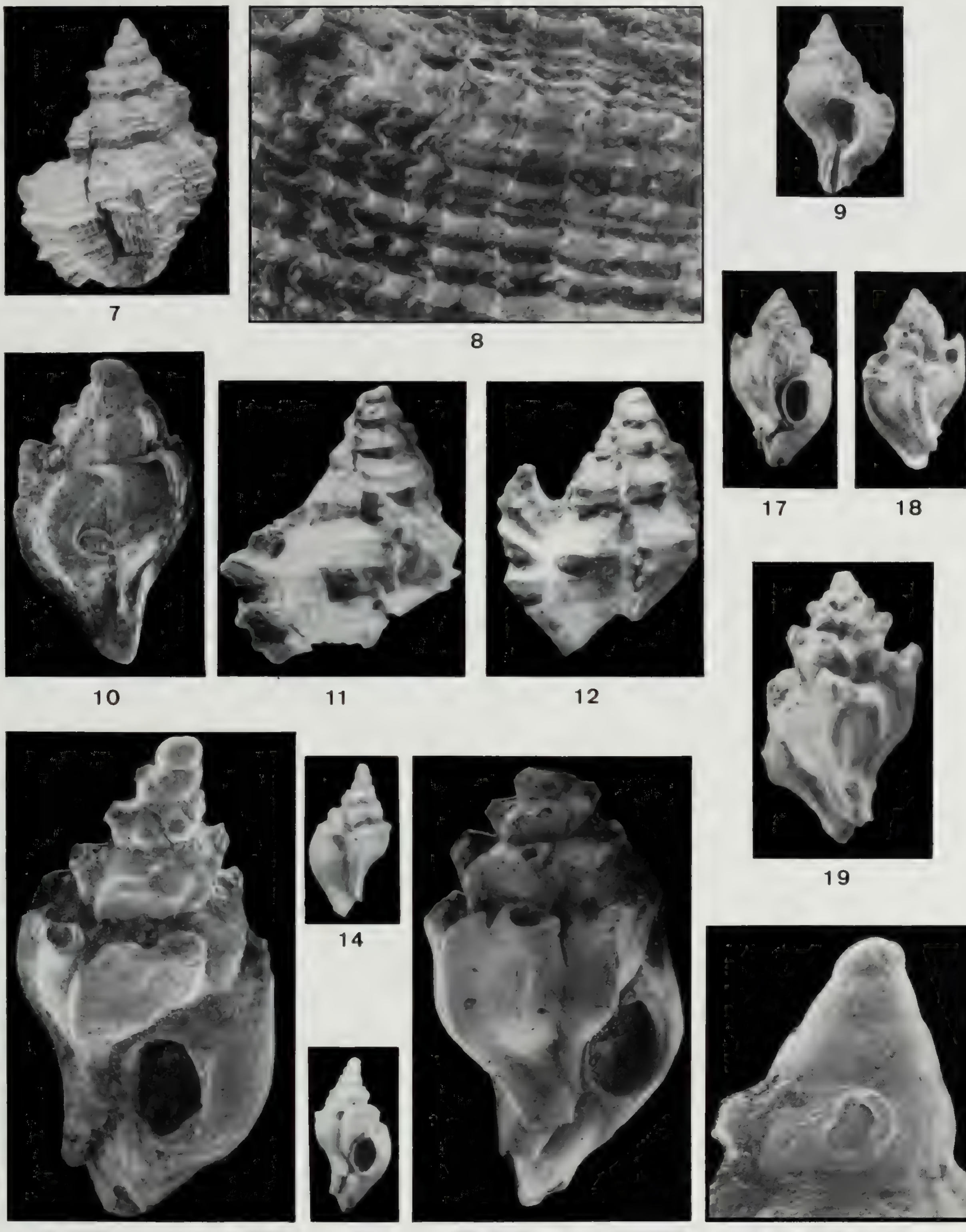
Figures 7-20 (ci-contre).
7 - *Chicoreus (?) subfiligrana* (Tournouër *in* de Bouillé, 1876), néotype, collection Neuville (UBX, n°TYFIPAL 57.2.1), H: 15 mm.
8 - *C. (?) subfiligrana* (Tournouër *in* de Bouillé, 1876), collection Cossmann n°16453a (MNHN-LP n°J00001), détail de la microsculpture du labre, X 20.
9 - *Pterynotus (Pterynotus) crenulatus* (Röding, 1798), collection Neuville (UBX, n°TYFIPAL 57.2.2), H: 9,55 mm.
10 - *Pterynotus (Pterynotus)* cf. *consobrinus* (d'Orbigny, 1852), collection Tournouër (IGAL), très jeune individu montrant une protoconque paucispirale, H: 3,3 mm.
11 - *P. (P.)* cf. *consobrinus* (d'Orbigny, 1852), collection Cossmann n°16453a (MNHN-LP n°J00002), individu plus âgé, H: 11,5mm.
12 - *P. (P.) consobrinus* (d'Orbigny, 1852), collection Merle, spécimen de Gaas (Stampien, Landes), H: 18,0 mm.
13 - *Siphonochelus (Laevityphis) biarritzensis* nov. sp., collection Neuville (UBX, n°TYFIPAL 57.2.3), holotype, vue montrant la protoconque et les premiers tours, H: 6,20 mm
14, 15 - *S. (L.) biarritzensis* nov. sp., collection Neuville (UBX, n°TYFIPAL 57.2.3), holotype, H: 6,2 mm.
16 - *S. (L.) biarritzensis* nov sp., collection Cossmann n°14276 (MNHN-LP n°J00003), paratype, H: 8,6 mm.
17, 18 - *S. (Trubatsa) evainae* nov. sp., collection Neuville (UBX, n°TYFIPAL 57.2.4), holotype, H: 9,65 mm.
19 - *S. (T.) evainae* nov. sp., collection Castex (BIA), paratype, H: 7,45 mm.
.20 - *S (T.) evainae* nov. sp., collection Cossmann n°14276a
(MNHN-LP n°J00004), protoconque X 45.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A review of the genus *Fulvia* Gray, 1853 (Mollusca, Cardiidae).

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KEYWORDS. Mollusca, Bivalvia, Cardiidae, *Fulvia*, review.

ABSTRACT. The Cardiid genus *Fulvia* is revised based on examination of type material and over 900 lots in relevant museums. Characters of shell sculpture are regarded as taxonomically more reliable than shape and colour, hitherto the base of specific taxonomy in the genus. It is established that *Fulvia* shares with *Vepricardium* numerous characters, including the presence of ocular organs on siphonal tentacles, and is included here in the tribe VEPRICARDIINI. *Laevifulvia* subgen. nov. [Type species: *F. undatopicta* Pilsbry, 1904] is segregated from *Fulvia* s.s., based on the lack of periostracal insertions on the ribs. Sixteen Indo-Pacific species of recent *Fulvia* are recognized, of which six are new. The name *F. papyracea*, hitherto used for a common Indo-West Pacific species is shown to represent a rare and restricted species. The name *F. fragilis* (Forsskal in Niebuhr, 1775) is to be used for most usages of *F. papyracea* of authors.

RESUME. Révision du genre *Fulvia*, famille CARDIIDAE, basée sur l'examen du matériel type et de plus de 900 lots de différents muséums. Les caractères de l'ornementation de la coquille sont considérés comme taxonomiquement plus fiables que la forme générale ou la couleur, sur lesquelles, jusqu'à present, les séparations spécifiques sont basées. Il est constaté que les *Fulvia* partagent avec les *Vepricardium* de nombreux caractères, en particulier la présence d'organes oculaires à l'extrémité des tentacules siphonaux, et sont donc placées ici dans la tribu des VEPRICARDIINI. On sépare de Fulvia s.s. un sous genre *Laevifulvia* [Espèce type *F. undatopicta* Pilsbry, 1904], séparation basée chez ce dernier sur l'absence d'insertions périostracales sur les côtes. Il est reconnu seize espèces récentes de *Fulvia* dans l'Indo-Pacifique, dont six sont nouvelles. On montre que le nom *Fulvia papyracea*, utilisé jusqu'ici pour désigner une espèce commune de l'Ouest de l'Indo-Pacifique, représente en réalité une espèce rare et d'extension limitée. Le nom *F. fragilis* (Forsskal in Niebuhr, 1775) doit êre utilisé, la plupart du temps, à la place de *F. papyracea* utilisé par les auteurs.

INTRODUCTION

This general study originates from an attempt to identify some species of the genus *Fulvia* found around New Caledonia. For these identifications I both consulted literature and compared identified specimens in museums. The result was very confusing and I remained perplexed about the true identity of many forms at the specific level, the generic level always being easy to determine. The literature on this subject is of little help because the descriptions are always too succint, the effective comparisons quasi-absent, and opinions often vary from an author to another. In the museums the identifications are also often rather disconcerting. I then presumed that the reason of this confusion could be the inconsistency of the characters in the species of this genus. As a matter of fact, they are generally reputed to be very polymorphic and, although there are twenty five nominal species, the most recent authors have been prudently inclined to consider only a small number of species (about four or five) in this group, and FISCHER-PIETTE (1977) admits the existence of only two species of recent *Fulvia*!

MATERIAL AND METHODS

In the literature, the criteria for description and species separation are scarce and rather vague and subjective. They mainly concern the general shape of the shells, the colours and the strength of the ribs, characters which, at first sight, look variable in a same species and may be common to several. The review of the genus *Fulvia* consisted of examining systematically in each specimen the largest number of characters, beside shape and colours, in order to find

characters with significant taxonomic importance.

The type specimens are very rarely cited and can often be supposed as not having been taken into account by the authors. Almost all the extant types specimens have been examined.

For this study about 905 lots have been examined and ,in almost half this number, at least one, often several specimens, have been measured. In this material, about 588 lots originate from ORSTOM's dredging program conducted by B. Richer de Forges in the peripheral lagoon of New Caledonia and in the shallows of Chesterfield Islands, from 1984 to 1992. This material is in the MNHN.

This material comes from the following museums:

AMS: Australian Museum - Sydney.
ANSP: Academy of Natural Sciences - Philadelphia.
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MNHN: Museum National d'Histoire Naturelle - Paris.
NM: Natal Museum - Pietermaritzburg.
QM: Queensland Museum - Brisbane.
WAM: Western Australian Museum - Perth.
ZMA: Zoologisch Museum - Amsterdam.
ZMUC: Zoologisk Museum - Copenhagen.

DEFINITIONS

In order to simplify the descriptions, some expressions are used, defined as follows:

A = Angle A: In the right valve, the angle between two lines joining the main cardinal tooth to the laterals.

AT= Anterior Third of the shell in a radial division, excluding the lunule *sensu stricto* and the sublunule (pl. 1, fig. 1).

When the sublunule is long this "third" is reduced.

D = Ratio D: In the left valve, the ratio between two distances: the distance from the extremity of the posterior lateral to the tip of the umbo and the distance from this point to the middle of the anterior lateral.

Granulation, granules (pl. 1, figs. 4 and 8; pl. 2, fig. 10; pl. 3, fig. 7): Minute tubercles very often present on the external surface of the shell. They can be concentrically aligned, sometimes on long distances (several ribs and interstices). They are usually situated on the anterior half of the shell but can be present everywhere. These small tubercles have an hexagonal symmetry in most species.

IMR = Internal Marginal Ribbing: The reverse of the external ribbing extending onto the internal side of the shell at the margin and in a certain distance from it. This "ribbing" is always well discernible and the comparison of the width between ribs and interstices (which is an important taxonomic character) is always easier to observe in the IMR.

Intersticial riblets: In the posterior third of the shell, more or less numerous small ribs, often irregular, can appear in the interstices between the main ribs (pl. 1, fig. 8).

Last flat: On the external posterior part of the left valve, the area, often relatively wide, between the last rib and the dorsal margin, bearing the posterior lateral on its inner side. This zone is generally flat or slightly concave (pl. 1, fig. 8).

Last fold: On the external posterior part of the right valve, the area, often relatively wide, between the last rib and the dorsal margin, bearing the posterior lateral on its inner side. This zone is generally convex. When the shell is closed, the last fold partially overlaps the last flat (pl. 1, fig. 8).

Lunule: It is not a true lunule (present only in FRAGINAE) but the most anterior part of the shell, always without ribs and periostracal insertions, often separated from the rest of the shell by the perilunular furrow (see this word). The smooth zone can extend farther backwards (sublunule), but, in the descriptions, the lunule *sensu stricto* will be limited at the level of the extremity of the basement of the anterior teeth, even when a furrow is not present, and its "length" along the margin will be measured from this point to the extremity of the umbo (pl. 1, fig. 1).

Lunular heart: The anterior dorsal margin of the shell just beside the umbo, exteriorly arising and spreading on both sides, forming like a "heart" (pl. 1, figs.2 and 3).

Ocular organs: Situated on the tip of tentacles bordering the two siphonal apertures; they are generally darker.

MT = Medial Third in a radial division (pl. 1, fig. 1).

Perilunular furrow: The lunule *sensu stricto* is sometimes limited by a more or less large and deep furrow, a slight and open groove corresponding internally to the ridge supporting the anterior tooth.

Periostracal insertions: In most species, periostracal lamellae are perpendicularly implanted in the shell on or along the ribs. These insertions consist of a succession of elementary components formed with short concentric lamellae and longer radial ones, forming "nodes" at their intersection, with a simple (pl. 1 ,fig. 5) or complex arrangement (pl. 1, fig. 7) according to the different species. Joined end to end these basic elements form finely undulating or zigzagging palisades on or along the ribs. These fragile palisades often disappear when the shell dries, but the traces of the insertions are always visible on the surface of the shell. Sometimes the nodes become calcified and form tubercles or spines on the ribs (pl. 1, fig. 6).

Posterior groove: Most species have a distinct more or less pronounced radial groove in the middle of the posterior third of the shell forming a notch in the margin and corresponding interiorly to a raised radial oblique ridge.

PT = Posterior Third of the shell in a radial division, often divided into two parts by the axis of the posterior groove (see above): PT1: the anterior part, close to the MT and PT2: the posterior part, ending beside the last flat or the last fold. Often, these two parts of the PT have distinct ribs (pl. 1, fig. 1).

Sublunule: In some species the lunule *sensu stricto* is followed by a more or less developped area without ribs nor IMR, but with some possible periostracal insertions. This area is sometimes separated from the lunule by a "perilunular furrow" (see this word). The length of the sublunule along the margin will be estimated by comparison with the length of the lunule (pl. 1, fig. 1).

TAXONOMY OF THE GENUS *FULVIA* GRAY, 1853

The taxon *Fulvia* was created as a monotypic genus of the family "CARDIADAE" by GRAY (1853: 40), with a type species: *Fulvia aperta* Bruguière, from the Indo-Pacific. Also Gray cites another genus: *Papyridea* Swainson, 1840, for which he had designated the type species (1847: 185): *Papyridea soleniforme*, from the American Atlantic. In spite of these clear, logical and unambiguous definitions, and in spite of the fact that these two species, the gaping excepted, are extremely different, the majority of the subsequent authors did not follow Gray and, for a long time, *Fulvia* was erroneously considered as a subgenus of *Papyridea*. In 1951, KEEN justly separated both taxa: *Papyridea* was placed, as a genus, into the subfamily TRACHYCARDIINAE and *Fulvia*, as a subgenus of *Laevicardium*, into the subfamily LAEVICARDIINAE Keen, 1951. [The erection of LAEVICARDIINAE by KEEN (1936: 367) does not comply with ICZN art.13,(a),(i), and is nomenclaturally unavailable]. KAFANOV & POPOV (1977: 310) consider *Fulvia* and *Laevicardium* as two genera of the tribe LAEVICARDIINI, subfamily CARDIINAE. Finally, SCHNEIDER (1992: 146), again places *Fulvia* and *Laevicardium* into the subfamily LAEVICARDIINAE.

Nevertheless, several authors, for example WILSON & STEVENSON (1977: 52), have noted that "the species of *Fulvia* do not agree with the diagnosis of *Laevicardium*" for many reasons. This study confirms the veracity of this opinion and it can be remarked also that the species of *Fulvia* have numerous affinities with the species of *Vepricardium* Iredale, 1929. These similarities are as follows:

1)- Shape comparable, with length more or less equivalent to height, often equilateral with rounded margins and no or limited posterior truncation.

2)- Hinge similar with, in particular, a large angle A.

3)- Several other features are comparable in both groups: large lunule with a lunular heart, well developped last fold overlapping a last flat etc...

4)- Young specimens of *Vepricardium* are also radially divided into three parts, with a smoother median one, and can look very much like *Fulvia*.

5)- Young specimens of some *Vepricardium* bear also "periostracal insertions", which turn into calcified palisades or spines in the adults, with equivalent detailed structures.

6)- In some species of *Fulvia*, the nodes of the periostracal insertions change into calcified spines, like those of *Vepricardium*.

7)- The external surface of the shell, in both groups, bears numerous minute granules, often concentrically aligned.

8)-The last but maybe the most significant element of similarity: the presence in both groups of ocular organs (see above). As far as I know, this character does not exist in the other

CARDIIDAE, except in the two species of the European genus *Cerastoderma*.

Because of these numerous affinities, I think that *Fulvia* and *Vepricardium* must be placed into a same suprageneric group and logically into the tribe VEPRICARDIINI, subfamily CARDIINAE (see later).

As far as *Laevicardium* s.s. is concerned, the species of this genus remain similar to *Acrosterigma* Dall, 1900, as far as certain characters are concerned, and should be placed into the tribe TRACHYCARDIINI Stewart, 1930. Nevertheless, it is true that some characters of *Laevicardium* are present in some evolved species of *Fulvia* (particularly in the subgenus *Laevifulvia*). I think this is due to a phenomenon of convergence.

In brief the taxonomy of *Fulvia* is considered here as follows.

Family CARDIIDAE Lamarck,1809,
Subfamily CARDIINAE Lamarck,1809,
Tribe VEPRICARDIINI
Kafanov & Starobogatov
(in Kafanov & Popov, 1977).

Genus *Fulvia* Gray, 1853.

Type species: *Fulvia aperta* (Bruguière).

General characters: Shell often thin and fragile, more or less translucent, but sometimes moderately thick and opaque. Dimensions variable from small (10 mm) to large (100 mm) in length.

Shape: Rarely noticeably elongated (length generaly nearly equivalent to height), varying from subcircular and equilateral to inequilateral, with the posterior side more or less transversally to obliquely expanded. Sometimes slightly truncated on the posterior margin, the anterior and ventral margins being always rounded. Variably but rather moderately inflated, with a regular general concentric curvature of the shell (no or exceptional medio-posterior accentuation of the curvature nor rostration). Often, presence of a "posterior groove" (see above). The shells are generally practically closed in the posterior margin, only two species noticeably gaping.

Other external features: (See above for certain definitions). Umbo generally prosogyrate without exaggeration. "Lunule" generally broad, with a variably developed "lunular heart". "Sublunule" from nonexistant to extremely well developped. Presence of a "last flat" and a "last fold", both of variable extention and profile.

Colours: Exterior of the shells of variable colour: white, beige or yellowish to orange, brown purple, with often, mainly in the young shells, more or less developed darker irregular concentric stripes or zigzags dark yellow, brown to pink or purple.The tip of the umbo is often coloured purple, and also sometimes the sublunule and part of the posterior third.

Interior generally white, beige to orange often with more or less developed irregular concentric stripes corresponding to those in the exterior and also one or two thin radial lines crossing the above stripes. Posterior zone often coloured purple. Sometimes the interior is almost entirely coloured pink, orange, brown or purple, and sometimes only in the umbonal cavity.

Sculpture:

a)- Number of ribs: This number is extremely variable between the species, and within some species according to populations and individuals. It ranges between 33 and 68.

b)- Ornamentation:

The young shells (and the earliest formed part of the adult shells) are smooth, except for some large ribs in the PT1. When the shell grows, ribs and interstices appear progressively in the other parts. They are always the strongest and the largest in the PT and the weakest in the MT, where they can sometimes be hardly perceptible. Nevertheless the internal marginal features (IMR, which have a significant taxonomic interest) are obvious everywhere.In the PT some irregular interticial riblets can appear in the interstices. In some species the ribbing and the IMR disappear in the most anterior part of the shell, behind the lunule (sublunule more or less developed).

The profile of the ribs and interstices varies according to the species and to the position on the shell. The ribs are often flat, with rounded edges, but can be triangular or rounded. They are generally smooth, without any ornaments, but in some rare species tubercles can appear. The interstices are generally flat and of very variable width with regard to the ribs. They are generally smooth but they can be striated in the PT.

In most species the ribs bear "periostracal insertions". They are generally located on the posterior limit of the ribs, but they can be placed in a variable position from this limit to the middle of the rib. When they exist, these insertions are present on all the ribs of the shell. They sometimes remain also in the sublunule, although the ribs and IMR have disappeared.

In some species, one, sometimes two, periostracal insertions develop on the last flat or the last fold.

The external surface of the shell is almost always ornamented with minute tubercular granules, often not perceptible with the naked eyes. These microscopic pustules mostly develop in the anterior part of the shell, but they can be present everywhere. They are often concentrically aligned. They can be limited to the interstices, or to the ribs, or to be placed on both.

Hinge: Hinge plate narrow, thin, moderately curved (angle A varying from 150° to 120°), occasionally angled in its anterior part, rarely excessively assymmetric (ratio D generally varying from 1.0 to 1.2, but sometimes reaching more extreme values: 0.8 to 2.0).

Cardinals generally unequal and separated in the left valve, approximately equal and touching at their base in the right valve.

Posterior lateral in the left valve very low, elongated, blade-like, often hardly separated from the ventral margin; in the right valve this tooth is higher and triangular. The main anterior lateral in the right valve is thin, pointed and triangular; it is prolonged towards the umbonal area below the hinge plate, forming a very regularly arced well delineated ridge, flattened against the internal surface of the shell. In the left valve the anterior lateral is roughly triangular and is prolonged by a raised narrow ridge, more or less elevated, separated from the dorsal margin by a deep elongated cleft which reaches the cardinal area. The ventral border of the above internal ridges limiting the anterior laterals corresponds exactly with the limits of the lunule.

Soft parts: The softs parts of ten species (of sixteen) have been observed, plus one literature record. All have two siphonal apertures bordered by tentacles, and some of these tentacles always bear dark ocular organs on their tip.

The genus *Fulvia* will here be separated into two subgenera:

Subgenus *Fulvia*

Type species: *Fulvia aperta* (Bruguière).
Diagnosis: See general diagnosis of the genus *Fulvia*, periostracal insertions present.

Subgenus *Laevifulvia* new subgen.

Type species: *Fulvia undatopicta* (Pilsbry).
Diagnosis: See general diagnosis of the genus *Fulvia*, but no periostracal insertions.

SPECIES LIST AND IDENTIFICATION KEY

A)- *Fulvia (Fulvia)*: Periostracal insertions.

1a: Presence of a rather long sublunule **2**
1b: Very short or no sublunule **3**

2a: Sublunule as long as the lunule:
Fulvia (F.) dulcis (Deshayes, 1863): Small, equilateral, large lunular heart, irregularly coloured, ribs in AT and MT hardly perceptible, ribs strong in PT.
2b: Sublunule shorter than the lunule:
Fulvia (F.) scalata sp. nov.: Small, equilateral,, very large lunular heart, uniformly coloured, ribs strong in PT and AT, perceptible in MT. Granules in AT and PT aligned like rungs of ladder in the interstices. Triangular nymph.

3a: In MT, ribs and interstices of unequal width **4**
3b: In MT, ribs and interst. of about the same width **6**

4a: In MT and part of AT, ribs very much wider than interstices:
Fulvia (F.) mutica (Reeve, 1844): Large to v. large, uniformly coloured, ribs in MT very weak but IMR well marked. Periostr. insertions strong, always placed in the middle of the ribs. No granulation in adult specimens.
4b: In MT and part of AT, ribs very much narrower than interstices **5**

5a: Shell equilateral, not gaping:
Fulvia (F.) papyracea (Bruguière, 1789): Large, ribbing very weak in MT, numerous granules in AT, hinge regularly curved, ratio D about 1.2.
5b: Shell inequilateral, gaping:
Fulvia (F.) aperta (Bruguière, 1789): Large, lunule large, ribbing very weak in MT, granulation in AT, hinge anteriorly angled, ratio D about 1.0 or less.

6a: Ribs and interstices not flat (rounded or triangular) **7**
6b: Ribs and interstices flat **9**

7a: Shell fragile, gaping, dark colour, discretely ribbed:
Fulvia (F.) natalensis (Krauss, 1848): Medium to large, inequilateral, lunule very small, ribbing regular on the whole shell, no granulation, hinge not angled, ratio D very high (1.4 to 1.9).
7b: Shell solid, closed, light colour, markedly ribbed **8**

8a: Ribs flatly rounded to asymmetrically triangular in MT, rather rounded in AT:

Fulvia (F.) fragilis (Forsskal, 1775): Medium to large, last fold high and regularly rounded, 41 ribs (34-52), calcareous spines in PT2, granules only in young shells very anteriorly.

8b: Ribs symmetrically triangular in MT, rather triangular in AT:

Fulvia (F.) tenuicostata (Lamarck, 1819): Medium to large, last fold very large with two parts (round and flat), 51 ribs (44-59), No calcareous spines in PT2. Granules rather rare in AT.

9a: Elongated calcified tubercles in PT:

Fulvia (F.) boholensis sp. nov.: Medium, inequilateral, generally orange, IMR in MT often almost indistinct.

9b:No calcified tubercles in PT **10**

10a: Shell small, roundly angled between MT and PT:

Fulvia (F.) fragiformis sp. nov.

10b: Shell medium, with regular concentrical curvature:

Fulvia (F.) australis (Sowerby, 1834): More often than not obliquely inequilateral, in MT and AT: identical weak flat regular ribbing, strongly constrasting with the one in PT, much wider and stronger and rather irregular.

B)- *Fulvia (Laevifulvia)*: No periostracal insertions:

1a: Shell elongated when adult, higher than long **2**

1b: Shell not elongated. **3**

2a: Sublunule about as long as lunule:

Fulvia (L.) undatopicta (Pilsbry, 1904): Small, equilateral, often 4 "crushed" spots, numerous aligned granules in AT.

2b: Sublunule much longer than lunule:

Fulvia (L.) lineonotata sp. nov.: Small, inequilateral, coloured by small aligned triangles, thin granules in AT.

3a: Shell longer than high:

Fulvia (L.) hungerfordi (Sow, 1901): Small, asymmetric, "polygonal" aspect, granules on the whole shell, ribbing and IMR in MT variable.

3b: Shell as long as high. **4**

4a: Shell small, very inequilateral:

Fulvia (L.) prashadi sp. nov.: Ridged and strongly separated sharpened PT, No ribbing nor IMR in MT, strong in PT, very rare or no granules.

4b: Shell medium, almost equilateral:

Fulvia (L.) ballieni sp. nov.: Regular weak ribbing and IMR in MT and AT, larger ribbing in PT. Granules on the umbo.

SPECIES DESCRIPTIONS.

Fulvia (Fulvia) aperta (Bruguière, 1789) (pl. 1, figs. 9a-b; pl. 2, fig. 7).

Cardium apertum sive hians, testa tenui etc... Chemnitz, 1782 :189, pl.18, figs. 181-183 (Not binominal).

Cardium apertum Chemnitz: Bruguière, 1789: 226.

Synonyms:

Cardium "rogata" (sic) Gronovius, 1781: 266 and Index No 1125, pl. 18, fig. 5 (Not binominal).

Cardium hians Spengler, 1799: 39.

Cardium rugatum "Gronovius": Dillwyn, 1817: 125.

Questionable synonyms:

Cardium virgineum Linn,, 1758: 682. (See Dodge 1952: 67).

Cardium bullatum Linn,, 1758:673. (See Dodge 1952: 37, 68).

Types:

C. apertum: Bruguière's 1789 description is based only on Gronovius and Chemnitz, and the only shells cited are the ones figured by these authors. Gronovius' specimen has not been traced, but Chemnitz's specimen is still in the ZMUC, Spengler collection, Ref. BIV 42. It is erroneously located from Jamaica. Dimensions: H=48.6, L=48.1, W=30.5. D=1.0. With 44 ribs. This shell is here selected as **lectotype** of *Cardium apertum* (pl. 1, figs. 9a-b).

C. rugatum: The specimen figured by Gronovius was not located.

C. hians: Spengler had two **syntypes** in his own collection of this nominal species, now in the ZMUC: the specimen BIV 42 above cited, and another specimen BIV 43. Dimensions of the latter: H=43.6, L=44.4, W=29.3. D=0.92. With 44 ribs. The specimen BIV 42 is here selected also as **lectotype** of *Cardium hians*, so this taxon becomes an objective synonym of *C. apertum*.

C. virgineum and *C. bullatum*: no type specimens located.

Description:

Shell of medium size, up to 48 mm in length.

Shape relatively constant, inequilateral, with its anterior side short and rounded and its posterior side transversaly expanded, often

slightly truncated and always raised at its extremity, causing a significant gaping (pl. 2, fig. 7). Sometimes, the flattening of the lunular area sharpens the anterior side a little. No or very weak posterior groove. Length always a little greater than eight.

Lunule very large, with a significant perilunular furrow. No lunular heart. No sublunule. Last flat present, but small, in the young shells only; when the shells become adult it decreases progressively in width, then disappears. Last fold rounded, high but narrow, without periostracal insertions.

External colour variable, uniformly whitish or beige or with irregular concentric zones of purple red to brown, sometimes only spotted with these colours. The density of the coloured zones generally decreases with the growth of the shell. Umbo often purple.

Internal colours generally the same by transparency except in the posterior area, almost always purple coloured. Sometimes, presence of a thin radial red strip in the umbonal cavity.

Mean number of ribs 43 (range 39-48).

In the whole AT and MT zones, the ribs are triangular, very narrow, and the interstices flat and comparatively very large. . In the PT1 the ribs become flatly triangular, increasing in width, and in the PT2 they become equivalent to the interstices. The IMR extends far from the margin.

The periostracal insertions are always situated in the posterior side of the ribs, and form complex arrangements.

Granules very numerous, more or less aligned on short distances, present only on the AT or the anterior half of the shell.

The hinge line has two specific characteristics: First, and paradoxically, its posterior side is relatively short (ratio D = approximatively 1 or less). Secondly, it is appreciably angled in the middle of its anterior part (and not at the level of the umbo, like in the other species).

Ocular organs observed.

Material examined and distribution: The type specimens listed- Other lots: OMAN: Gulf of Oman: 1 MNHN- MAURITIUS: 1 ZMUC- THAILAND: Phuket: 1 ANSP; 2 MNHN- THAILAND: Gulf of Thailand: 1 MHNG- MALAYA: Srait of Malacca: 1 WAM; Gulf of Thailand: 1 WAM- PHILIPPINES: 2 MNHN; 6 ANSP- HONG-KONG: 1 MNHN; 1 BM(NH)- CHINA: Hainan: 1 MNHN- JAPAN: 2 MNHN- INDONESIA: Java: 1 MNHN- MALAYA: N. Borneo: 1 ANSP- PAPUA: 1 ANSP- AUSTRALIA: 1 MNHN- Queensland: 2 MNHN; 3 ANSP- W. Australia: 1 MNHN; 3 ANSP; 1 ZMUC- NEW CALEDONIA: 9 MNHN; 3 ANSP- SOLOMON: 1 ANSP. The lots from the Eastern Indian Ocean are rather scarce, more numerous from Western Indian Ocean and Western Pacific.

Habitat: In New Caledonia it prefers littoral muddy organic environments.

Observations: *Fulvia aperta* is easily distinguished from the other species of the genus mainly by its gaping which is exceptionally absent, but also by its ribbing and the characters of its hinge.

Fulvia (Fulvia) papyracea

(Bruguière, 1789)
(pl. 1, figs. 7, 10a-b and 11a-b)

Cardium papyraceum, testa cordata, fragili etc... Chemnitz, 1782: 190, pl. 18, fig. 184 (Not binominal).
Cardium papyracea Schröter, 1788: 82 (Not binominal).
Cardium papyraceum Chemnitz: Bruguière, 1789, Vers, I: 231.

Synonym:
Fulvia voskuili Healy & Lamprell, 1992: 89-91, pl. 4, figs. a-d. [= *F. sp.* : Lamprell et al., 1992, n° 226].

Questionable synonym:
Cardium pallidum Reeve, 1845: Sp 92, fig.92.

Types:

Cardium papyraceum: The description of Bruguière is just a translation of Chemnitz and the only shell cited is the one figured by the latter (pl. 18, fig. 184). This **holotype** is still preserved in the ZMUC, No BIV 44, Spengler collection. The old labels indicate "Jamaica", but Chemnitz gives East Indies as locality. Dimensions: H=41.0, L=37.4, W=25.0. Angle A=125°, ratio D=1.4. With 42 ribs (pl. 1, figs. 11a-b).

Fulvia voskuili: Holotype in the QM reg. MO32906 (pl. 1, Figs. 10a-b), from Kelso Reef (N. Queensland), H=34.3, L=33.8, W=22.0, angle A= 130°, ratio D= 1.3, with 33 ribs. - **Paratype n° 1** in the AM (reg. C166907), from Dingo Beach (N. Qld.), H=31.0, L=31.0 W=20.6. - **Paratype n° 2** in the Museum of Victoria (reg. No F60471), also from Dingo Beach, H=28.0, L= 28.4, W=17.7.

Cardium pallidum: In the BM(NH), two shells are registered n° 1978.134 as **syntypes** of *C. pallidum*, considered as coming from the Bay of Manila, Philippines, Cuming collection. But,

as mentioned on the label: "none agree with figure and locality. Has been crossed out". These two shells look very much like *F. tenuicostata*, since the description, figure and locality of Reeve's specimen strongly suggest it is *F. papyracea*.

Description:

Shell of medium size, up to 45 mm in height.

Almost perfectly equilateral, rarely a little expanded backwards like the holotype. Rather depressed. No or very slight posterior truncation. Generally almost circular with L/H ratio very close to 1, the holotype being exceptionally a little elongated (L/H=0.91). No or very weak posterior groove.

Lunule large. No sublunule. Lunular heart small. Last flat relatively wide and flat. Last fold wide and flatly rounded.

External colour of the adult rather uniform, variable but almost always light, whitish to light brown, the young shell being more coloured with darker concentric stripes. Umbo often purple.

Internal colour whitish with more or less numerous brown-purple concentric stripes and often a thin radial purple line in the umbonal cavity. Almost always purple coloured in the posterior zone, this coloration being sometimes also perceptible exteriorly.

Mean number of ribs: 43 (range 37-48).

With the exception of the four or five last ribs of the PT2, the ribs are always much narrower than the interstices, which are wide and flat. In the AT, the ribs are very thin and triangular and become flatly rounded and hardly perceptible in the MT, then more perceptible in the PT1. In the PT2 the ribs are closer one from another with almost always well marked interstiicial riblets. The rib features of the AT and MT are discernible internally, but at the margin itself they are of variable distinctness.

Periostracal insertions, always located in the posterior side of the ribs, form complex arrangements (pl. 1, fig. 7).

Granulation always present on the anterior half of the shell.

Hinge and dorsal margin looking symmetrical on both sides, with a mean angle A of 134° and a ratio D of about 1.3.

Ocular organs: no data.

Material examined and distribution: The holotype of *C. papyraceum*, and the holotype of *F. voskuili*- Other lots: INDIA: Gulf of Manaar: 2 ANSP- MALAYA: Strait of Malacca: 1 ANSP- SINGAPORE: 1 MNHN; 1 ANSP- PHILIPPINES: 2 ANSP; Manila: 1 QM; Subic Bay, Luzon: 1 MNHN- INDONESIA: Amboina: 1 MHNG; Yapen Island: 1 ANSP; Schouten Island: 1 ANSP- AUSTRALIA: N. Qld, Shelburne Bay: 1 QM; Gulf of Carpentaria: 1 QM.

Other lots: In MNHN, one specimen in a lot of *F. australis* labelled from Mauritius (old collection, mixing ?). In ANSP, two lots whithout locality (54159,54198).

Observed also Lamarck's specimen in the MHNG (see below).

Observations: As mentioned by Chemnitz, *F. papyracea* is close to *F. aperta* in appearance: both have equivalent thinness, same colours and also approximately a same structure of ribs and interstices. But *F. papyracea* never gapes and has some other characters to distinguish it from *F. aperta*: symmetry of the shell and of the hinge, ratio D distinctly higher, lunular heart more developped, last fold and last flat wider, interstiicial riblets in the PT2 more frequent. *F. papyracea* is distinguished also from *F. mutica* which is larger and of different coloration, has a smaller lunule, much wider ribs with axial periostracal insertions, very different and typical IMR, and from *F. australis* mainly by its shape and its ribbing.

The name *papyracea* is particularly erroneously used for a form of Red Sea, Western Indian Ocean and Persian Gulf, here described as *F. fragilis*, which is incontestably different (see the description of this species).

F. voskuili has all the characters of *F. papyracea*, except for the rib number of the holotype (33) which seems too low. Nevertheless three other specimens examined have: 42, 44, 47 ribs, in agreement with the range of *F. papyracea*.

Although the name *papyracea* is the most used in the literature for the different species of the genus *Fulvia* (23% of all the citations according to the chresonymy of Fischer-Piette (1977:76, 78, 79), *F. aperta* and its synonyms excluded), *Fulvia papyracea* is a rather rare species with a limited area of distribution. In the literature, the subsequent citations corresponding undoubtedly to the species in question are also extremely rare. These are:

1)- LAMARCK 1819: 6. Locality: East Indies. The shell referred to is now in the MNHG, reg. No 1085/40. It is represented by a typical right valve.

2)- REEVE 1844, Sp 9, fig. 9. Locality: East end of the Island of Luzon (Philippines). Good description and figure.

3)- HIDALGO 1903: 344. Locality: Subic Bay, Island of Luzon (Philippines).The description is excellent. No illustration given.

Fulvia (Fulvia) mutica (Reeve, 1844)
(pl. 1, figs. 5 and 12a-b)

Cardium muticum Reeve, 1844, Sp 32, fig. 32.
Synonyms:
Cardium japonicum Dunker, 1860: 223, 1861: 28, pl. 3, figs. 1-6.
Cardium annae Pilsbry, 1904: 557, pl. 40, fig. 20.
Cardium tcheliense Debeaux in Pilsbry, 1904: 558.

Types:

Cardium muticum: The only type is the specimen 67 mm long, from Cuming collection, without locality, figured by Reeve, not traced.

Cardium japonicum: The type material of Dunker is now in the Senckenberg Museum in Frankfurt (see JANSSEN, 1993). It is a shell 73 mm long, from Japan.

Cardium annae: The type specimens are two valves in the ANSP (reg. No. 86319): one left valve H= 20 mm, broken, and one right valve H=25.3, L=27.2. This right valve is figured by PILSBRY, pl. 40, fig .20 and here in pl. 1, figs. 12a-b).

Cardium tcheliense: The specimen mentioned by Pilsbry, from China, is in the ANSP (reg. n° 54302). Its dimensions are: 24.4x26.3x17.7.

Description:

Fulvia mutica is the largest of all the known living *Fulvia*, reaching 100 mm in length.

Its shape is relatively constant, roughly "diamond-shaped", almost equilateral, often with the posterior side a little longer. Not truncated but rather a little sharpened. The length is always a little larger than the height. Shell slightly gaping in the posterior side.

Lunule small, without perilunular furrow. No sublunule. Lunular heart extremely small. Last flat narrow and a little grooved. Last fold rounded, high and well separated, bearing or not a periostracal insertion.

External colour uniform, more or less dark beige. Internal colour white to purplish pink by zones.

Mean number of ribs: 47 (range 43-54). The ribs are weak but clearly discernible in the AT and the PT1, where they are flatly rounded and about equivalent in width to the interstices. In the PT2 they are very numerous. Towards the MT, the ribs tend to be wider and flatly triangular, and become more and more indiscernible. On the other hand, in the IMR zone (which does not extend very far from the margin), the "ribs" are well and finely marked, the "interstices" being very wide.

The periostracal insertions are thick and persistent; they are generally placed on the middle of the ribs. The insertion corresponds on the other side, in the IMR, to a very thin furrow on the middle of the "interstice" (very specific character). The insertions form a simple arrangement (pl. 1, fig. 5).

Granulation often present on the lunule and the AT in the young specimens (less than 10-15 mm), but never in the adults.

Hinge indistinguished, symmetric, with an obtuse angle A (range 135-150°). The ratio D varies from 1.2 to 1.4.
Ocular organs observed.

Material examined and distribution: The type specimens of C. annae and C. tcheliense- Other lots: CHINA: 1 ANSP; Kingdao: 1 MNHN- HONG-KONG: 1 ANSP- KOREA: 1 ANSP- JAPAN: 11 MNHN; 10 ANSP.

According to KIRA (1962: 210) the species extends from South-China to Alaska. REID & SHIN (1983: 281) indicate a southern limit around Yamaguchi (Japan).
Habitat: "Muddy bottom of sheltered waters" (KIRA, 1962: 210). Kira indicates also that " This is also one of the important edible shells in Japan".

Observations: *Fulvia mutica* can easily be distinguished from the other Fulvia by its particular "diamond-shaped" shape, its colours, but above all by its very particular ribbing and IMR.

Fulvia (Fulvia) tenuicostata
(Lamarck, 1819)
(pl.2, figs. 1a-b)

Cardium tenuicostatum Lamarck, 1819: 5, No 5.
Synonyms:
Cardium racketti Donovan, 1826: pl.124.
Cardium radiatum Reeve, 1845: Sp 89, pl.89.
Fulvia fagea Voskuil & Onverwagt, 1992: 42 (nomen novum for the latter).

Types:

Cardium tenuicostatum: There are three lots labelled by Lamarck in the MNHN. The first lot of two specimens 50.5 and 47 mm high, from Timor and New Holland. The second and the third lots with two and one specimen respectively, are somewhat different from the first lot (smaller and more equilateral) and respectively hand-labelled by Lamarck as "var." and "individual very young". I select the largest shell from the first lot as **lectotype**; its

dimensions are : H=50.5, L=54.0, W=30.7; number of ribs: 47, angle A= 138°, ratio D= 1.4. (pl. 2 , figs. 1a-b). The reference to Timor is very probably erroneous.

In Lamarck's collection of the MHNG, there is another specimen comparable to the main syntypes of the MNHN, but not hand-labelled by Lamarck, reg. n° 1085/38. It is 43.5x44.9x29.4, A= 140°, D= 1.2. This specimen, figured by DELESSERT (1841, pl.11, figs. 6a-c), must also be considered as a **paralectotype**.

Cardium racketti: The specimen figured by Donovan has not been traced.

Cardium radiatum: **Holotype** in the BM(NH), reg. n° 1912.6.4., from Hanley collection, locality unknown. H=32.3, L=34.3, W=23.8. Angle A=130°, ratio D=1.31. Number of ribs: 52.

Description:

Shell of medium size up to 56 mm in length, generally thick and solid in the adult stage.

Shape variable from almost equilateral to transversely and even obliquely expanded, often slightly truncated in the posterior side, which sometimes can be somewhat sharpened. Length always a little larger than height. No posterior groove.

Lunule small with no perilunular furrow. No sublunule. Lunular heart small. Last flat large. Last fold very large with two parts often separated by a small furrow: a rounded posterior part and a flat anterior one.

External colour light and uniform whitish to yellowish, rarely more or less concentrically mottled with darker colours. Umbo often purple coloured. Some specimens, a little differently coloured than usually, but in other respects typical, have been considered as specifically different (*C. radiatum* Reeve).

Internal colour white, sometimes with a red-purplish stain in the umbonal cavity and more rarely on the posterior ventral edge.

Mean number of ribs 51 (range 44-59). In the adult shells the ribs of the MT are as strongly marked as in the other two thirds. In the whole shell the ribs are equivalent in width with the interstices, or slightly wider.The ribs are generally more or less roundly triangular, often symmetrically. Rounded ribs can be present, but only in non adult shells.

According to the symmetry of the ribs, the periostracal insertions can be placed in the axis or more or less in the posterior part of the ribs. No periostracal insertion on the last fold. The nodes of the periostracal insertions never become calcified and spiny in the PT.

The granules are never abundant. They are present mainly in the young shells, in the AT.

No particularity in the hinge: mean A= 138°, mean D= 1.3.

Ocular organs observed.

Material examined and distribution: The type specimens of *C. tenuicostatum* and *C. radiatum*- Other lots: AUSTRALIA: 2 MNHN; 2 ZMUC; S.Eastern Australia: 3 MNHN; 5 AMS; 2 BM(NH); Southern Australia: 2 ANSP; 4 ZMUC; S.Western Australia: 4 MNHN; 2 AMS; 1 QM; 3 BM(NH); Tasmania: 2 MNHN; 2 QM; 2 BM(NH).

Southern Australia only. According to Wilson and Stevenson (1977: 55), "from the vicinity of Sydney on the East Coast to Fremantle in W.A".

Habitat: "Lives gregariously in sand and mud from two to 30m depth of water"(Ludbrook 1984:176).

Observations: *F. tenuicostata* differs from all the others (except *F. fragilis*) by having, when adult, a solid and thick shell with strong ribs in the MT. It is apparently close to *F. fragilis*, but both can easily be separated (see this species).

Fulvia fragilis (Forsskal in Niebuhr, 1775)
(pl. 1, fig. 6; pl. 3, figs. 1a-b)

Cardium fragile Forsskal in Niebur, 1775: 31.

Types:

Forsskal [in Niebuhr, 1775: 31] introduced the name *Cardium fragile* with the diagnosis: "*striatum transverse; tantum ad cardines laeve*". Although brief, this diagnosis qualifies as a description and the name *C. fragile* is nomenclaturally available. This opinion is shared by YARON et al.(1986: 95) who regard it as "eligible for standing as valid [taxon]". In ZMUC, there is a lot comprising 3 bivalves and one valve, originating from the Forsskal expedition to the Red Sea. This lot is without label and it is not absolutely certain that it corresponds to *C. fragile*. However, rather than naming a new species and leaving *fragile* forever in limbo, it seems preferable to stabilize this name by designating one of the Copenhagen's putative syntypes as neotype. I designate here the shell figured by YARON et al. (1986:194, fig 42) as **neotype** of *Cardium fragile*. This shell: H=23.6, L=23.0, W=15.9, with 44 ribs, angle A=120°, ratio D=1.6.

Description:

Shell of medium to large size up to 75 mm in height.

Shape generally approximately symmetrical, often with slight posterior truncation, but sometimes with the posterior part more or less transversally or obliquely expanded. Mean L/H a little higher than 1. Posterior groove weak to non existent. Sometimes very slightly gaping posteriorly.

Lunule large without perilunular furrow. No sublunule. Lunular heart variable but never large. Last flat wide and flat. Last fold very large and regularly rounded, bearing a periostracal insertion only in the young stage and in 50% of the specimens.

External colour generally uniform whitish, beige to yellowish, with a purple stain only on the umbo and sometimes on the lunular heart and on the last flat and fold.

Internally white, except on the posterior third which is almost always purple, and sometimes the umbonal cavity.

Mean number of ribs 41 (range 34-52). In the young shell, up to about 2 or 3 cm in height, the ribs of the MT are much less well marked than in the other thirds, like in the majority of the *Fulvia*, but in the fully adult shells they become as strong as the others.In the whole shell the ribs are equivalent in width with the interstices, or slightly wider. In the AT the ribs are generally rounded, but can sometimes become more or less symmetrically triangular. In the MT they become progressively asymmetrically triangular (posterior slope shorter and steeper), and can become practically flatly rounded. They remain more rounded in the PT1, but without transition they become more or less symmetrically triangular in the PT2 where the last interstices often bear intersticial riblets. In this latter area, the periostracal insertions become calcareous at the nodes, and produce tubercles or spines (pl. 1, fig. 6).

The periostracal insertions are always on the crest of the ribs in the AT; they progressively migrate to the posterior part of the ribs in the MT and also in the PT1; they migrate again on the crest of the ribs in the PT2. They form simple arrangements.

No granulation in the adult shells, but sometimes someones very dense on the lunule and the two or three first ribs of young specimens.

Indistinguished hinge: mean A= 138°, mean D rather high = 1.5.

Ocular organs observed.

Material examined and distribution: The type material- Other lots: EGYPT: Mansaleh lake: 1 MNHN; Timsah lake: 3 BM(NH); Great lake: 1 ANSP; Suez canal: 1 MNHN; Gulf of Suez: 11 MNHN- ISRAEL: Elat: 1 MNHN; 1 ZMUC- Red Sea (EGYPT, SUDAN, ERITREA, ARABIA, YEMEN): 6 MNHN; 2 AMS- DJIBOUTI: Gulf of Tadjoura: 5 MNHN- YEMEN: Aden: 2 MNHN- OMAN: Gulf of Oman: 2 MNHN- South Persian Gulf (TRUCIAL COAST, QATAR, BARAIN): 3 MNHN; 3 AMS; 1 ANSP; 1 BM(NH); 5 ZMUC- N. SOMALIA: 3 MNHN- KENYA: 1 MNHN- ZANZIBAR: 1 MNHN- MOZAMBIQUE: 1 MNHN; 1 ANSP; SOUTH AFRICA: Natal: 2 MNHN; 2 BM(NH)); 2 NM- ANGOLA: Luanda: 4 MNHN- CONGO: Pointe Noire: 4 MNHN- GHANA: Accra: 1 NM- COTE D'IVOIRE: 1 MNHN.

The species migrated through the Suez Canal and is present in the Mediterranean coast of Israel, together with *F. australis* (see Barash & Danin 1992: 275). The status of the populations found in the Atlantic Ocean will be discussed by Dr. von Cosel in a separate paper.

Habitat: Littoral to shallow water.

Observations: The first figuration of this species was in SAVIGNY's plates (1805-1812: pl. 13, fig. 9). AUDOUIN (1827: 200) named these figures only: *Cardium*....Subsequently *Fulvia fragilis* has generally erroneously been named *F. papyracea*, and sometimes *F. tenuicostata*. It differs from the former mainly by the thickness of the shell and strength of the sculpture, the larger width and different profile of the ribs and the absence of granulation, and from the latter by the lower number of ribs, the presence of rounded ribs in section, periostracal insertions situated on the posterior side of the ribs, rarely observed in the Australian species, and by some characters of the lunule and posterior flat and fold. It can be separated from *F. australis*, with which it is sympatric (except in the Atlantic Ocean), by its less oblique shape, its rounded and large instead of triangular and smaller last fold, its fewer ribs, the presence of well rounded ribs never observed in *F. australis*.

The distinction from the other species can also be helped, particularly with young specimens, by the presence in *F. fragilis* of "spines" in the PT2 and sometimes a periostracal insertion on the last fold. In other respects the young specimens seems to be variable as far as shape, proportions and colours are concerned and can look very different, from one to another and from the adults, which is often a little disconcerting.

Fulvia (Fulvia) natalensis
(Krauss, 1848)
(pl. 2, figs. 2a-b and 2c).

Cardium natalense Krauss, 1848: 12, pl.1, fig.9.
Cardium natalense var. *adjacens* Turton, 1932: 243, No 1710, pl. 65, fig. 8.

Types:

Cardium natalense: Krauss had only three small specimens and cited and figured one of them: H=14.6, L=16.6, W=9.0. These **syntypes** could be in the Stuttgart Museum.

Cardium natalense adjacens: Turton had only two tiny valves to define his subspecies, of which he selected the largest (6x8 mm!) as type. This **holotype** could be in the Oxford University Museum.

Remark: The present study is based on the examination of much larger and representative specimens, particularly from the lot n° 9576 Natal Museum, Kilburn collection, with numerous large specimens from Port Elizabeth (pl. 2, figs. 2a-b and fig. 2c).

Description:

Shell of medium size up to 43 mm in length.

Very inequilateral, with the posterior zone transversally expanded, rarely obliquely. Always longer than high: mean L/H= 1.12 (range 1.04-1.21). Anteriorly rounded and also posteriorly (never truncated). No posterior groove. Large posterior gape.

Lunule generally small to very small. No perilunular furrow. Lunular heart very little developed. Last flat narrow, concave. Last fold medium, flatly triangular, with always one, sometimes two, periostracal insertions.

External colour generally beige to light brown, more or less mottled with brown-purple, rather uniform, a little darker on the umbo.

Interior uniformly or irregularly dark brown-purple.

Mean number of ribs 45 (range 41-50). Ribbing rather regular, of the same strength on all the shell, the width of the ribs being everywhere equivalent to the one of the interstices, which is particularly visible in the IMR. The ribs are generally triangular and the interstices rounded. In the AT the ribs are symmetrically triangular and they become progressively asymmetric in the MT (posterior side shorter) and can become almost flat. In the PT the ribs are a little more rounded.

No granulation.

Periostracal insertions well marked, generally with predominance of the radial components, the concentric components often being absent or very small. The insertions are situated on the crest of the triangular ribs in the AT, migrating towards the posterior side in the MT, then coming back on the crest in the PT.

Hinge line slightly arced (A range 140-150°), without any angular break (difference with *aperta*). Left anterior lateral almost confused with .the margin and much more distant from the umbo than the anterior lateral (ratio D range 1.5-2.0).

Ocular organs: no data.

Material examined and distribution: S. MOZAMBIQUE: Inhambane Bay: 2 MNHN- SOUTH AFRICA: St Lucia Bay: 1 MNHN; Port Alfred: 1 NM; Jeffrey's Bay: 1 NM; Plettenberg Bay: 2 MNHN; Knysna Lagoon: 2 MNHN; 1 NM; Still Bay: 1 NM; Capetown: 1 ZMUC. Endemic of the south-Eastern coast of South Africa, from Port Alfred to False Bay.

Habitat: Mainly found in estuaries, in calm littoral waters of variable salinity, probably in muddy organic terrigenous facies.

Observations: *Fulvia natalensis*, often erroneously named as *papyracea*, has also been confused with *F. aperta* because of its gape. Nevertheless the latter differs in its less transversally expanded and less rounded shape, its lighter colour, its ribbing (ribs narrower than the interstices), its very much smaller ratio D, its larger lunule and its high and narrow last fold without periostracal insertions.

Fulvia (Fulvia) australis
(Sowerby, 1834)
(pl. 2, figs. 3a-b, 4, 5 and 6a-b)

Cardium australe Sowerby, 1834: fig. 12 and 1840: 105.

Synonym:

Cardium striatum Spengler, 1799: 45.

Questionable synonyms:

Cardium varium Sowerby 1834, fig 19.
Cardium pulchrum Reeve 1845, Sp 98, fig 98.

Types:

Cardium australe, varium, pulchrum: No type specimen referred to these three nominal species.

Cardium striatum: Two **syntypes** in ZMUC, Spengler collection, from South Seas. N° 1: 24.4x25.1x17.0, 50 ribs. N° 2: 23.8x23.8x15.5, 55 ribs.

Remark: The name *Cardium striatum* has priority over *C. australe*, but *australe* is used because: (a) *striatum* has never been used subsequently to Spengler, other than FISCHER-

PIETTE (1977: 160) in a list of "uncertain species"; (b) *australis* has been used over 50 times since its description, and is currently the second most widely used specific name in the genus *Fulvia*. (An application to conserve the name *F. australe* will be presented to the International Commission on Zoological Nomenclature).

Description:

Shell of medium size, up to 35 mm in height. The shells are generally thin, but rarely excessively, and are relatively solid.

Shape sometimes almost equilateral but generally obliquely ovate, inequilateral, with the dorsal anterior part inflated and the posterior part more or less obliquely expanded. Almost always slightly truncated in the PT2. Posterior groove generally well developed.

Lunule of medium size with a small lunular heart. Perilunular groove sometimes present. Sublunule often present but always short (equivalent of two or three ribs in length). This zone is very often red coloured, and bears periostracal insertions (it is therefore more easily discernible in the IMR). Last flat medium, sometimes concave. Last fold markedly triangular, mainly in the young shells, with no periostracal insertions.

Exterior colour very variable from pure white to dark brown purple. The young specimens (and the early formed part of the adult shells), are often more coloured, with generally darker, irregular, more or less concentrically arranged stains of variable density. The intestices are not stained, or are lighter coloured than the ribs.

Interior generally white to yellow or light pink, with the exterior darker stripes transparently visible and also some radial rays. Rarely presence of a slight reddish coloration in the posterior side.

The mean number of ribs is 49, but this number is extremely variable (range 34-68) between areas and populations (see below).

The ribs are similar and homogeneous in AT and MT, weakly marked, equivalent in width to the interstices or a little narrower, flat or very slightly rounded; interstices flat. In these two zones the IMR is also homogeneous and well marked. In the PT1 the ribs and interstices become irregular and the interstices become very wide with regard to the ribs which take a triangular profile. Intersticial riblets in the PT2 often present, but more or less well developed.

The periostracal insertions are always situated on the posterior limit of the ribs in the AT and MT, but tend to migrate to the crest of the triangular ribs in the PT.

Granulation of variable density, on individuals and populations, sometimes lacking, generally limited to the anterior half of the shell, on the ribs as well as in the interstices, sometimes aligned but always on short distances.

Hinge line and dorsal margin caracteristically asymmetric, with a receding posterior side and a raised and inflated anterior one , forming a vague angle like a hump. Angle A relatively "acute", mean value 133° (range 130-140), and ratio D rather high: mean 1.3 (range 1.2-1.5).

Ocular organs observed.

Material examined and distribution: The syntypes of *C. striatum*- Other lots: EGYPT: Gulf of Suez: 5 MNHN; Marsa Thlemel: 1 MNHN- ISRAEL: Elat: 1 ZMUC- DJIBOUTI: 2 MNHN- N. SOMALIA: 1 MNHN- OMAN: Gulf of Oman: 1 MNHN- ARABIA: S. Persian Gulf: 1 MNHN- KENYA: 1 MNHN- ZANZIBAR: 1 MNHN- TANGANYIKA: Dar-es-Salaam: 1 AMS- MOZAMBIQUE: Vilanculos: 1 MNHN- MADAGASCAR: E. coast: 5 MNHN; Dredging Tulear: 51 MNHN - MAURITIUS: 9 MNHN; 1 ZMUC- SEYCHELLES: 1 MNHN- INDIA: Gulf of Manaar: 2 ANSP- W. THAILAND: Phuket: 2 MNHN; 1 ZMUC; 1 ANSP- MALAYA: Tocal: 1 ZMUC- VIETNAM: 1 MNHN; Poulo Condor: 2 MNHN; Natrang Bay: 1 ZMUC- CHINA: 2 MNHN- JAPAN: 1 MNHN- PHILIPPINES: Manila 1 MNHN; Luzon: 1 WAM- AMER. PAC. TRUST TERR.: Nukuoro Atoll: 1 WAM- INDONESIA: Molucas, Cayeli: 1 MNHN- PAPUA: Hansa Bay: 2 IRSNB; Madang: 1 WAM- SOLOMON: 1 ANSP; 1 QM; 1 WAM- GILBERT: Kiribati: 1 AMS- TONGA: 1 MHNG; 1 WAM- FIJI: 3 MNHN; 1 WAM- VANUATU: 2 MNHN-NEW CALEDONIA: 113 MNHN; 2 ANSP- AUSTRALIA: 1 MNHN; Queensland: 2 MNHN; 2 AMS; 5 QM.

Found in the Suez canal and in the Mediterranean coast of Israel and Palestine, together with *F. fragilis* (see BARASH & DANIN, 1992: 275-276).

Habitat: littoral to shallow water. Seems to prefer clean reefal or perireefal facies.

Observations: *Fulvia australis* is the most common and widespread species of *Fulvia* and can be sympatric with almost all the others. It can easily be differentiated mainly by its very characteristic oblique asymmetry and the strong contrast between the ribbing in the AT and MT, dense, serried, regular and homogeneous, and the ribbing in PT, loose and irregular. As a

matter of fact it has not often been confused with the other species, unless in very young specimens. Nevertheless, in spite of its constant characters allowing always an accurate identification, this species can be variable in shape, colour and number of ribs.

A good illustration of this variability can be found in New Caledonia, where very numerous lots of this species are available, from several environments. It is possible to distinguish three forms:

1)- Forms comparable to the types of Sowerby and Reeve: shells of rather small size, slightly asymmetric, rather depressed (mean W/L = 0.65), strongly coloured outside and inside, with a small number of ribs (34 to 44). They are found mainly in the lagoon of the Ouvea atoll, at water depths from 10 to 20 meters. Such forms (with more ribs) exist locally in Australia, and sporadically elsewhere as individual variants. A specimen from a lot close to this form, from Shelburne Bay, North Queensland, lot QM No 45517, is figured here in pl. 2, figs. 6a-b: H=26.5, L=24.8, W=17.0, with 55 ribs.

2)- (pl. 2, fig. 5), shells of average size, mainly asymmetric, fairly depressed (mean W/L = 0.70), coloured by irregular concentric stripes of brown or purple (ribs only coloured, not interstices), and frequently with the umbo, the sublunule and the lunular heart purple coloured, an average number of ribs (40-55). Mainly in littoral zones. This form is the most common form of the species, found everywhere, more or less coloured, sometimes entirely white (see also pl. 2, fig. 4 an intermediate form).

3)- (pl. 2, figs. 3a-b), shells of rather large size for the species, almost symmetric, more globular (W/L up to 0.80), lightly coloured with or without darker stripes, with a large number of ribs (50-68), and no or rare granules. They are found mainly in the lagoon at water depths from 15 to 80 meters and exceptionally in the littoral zones. Comparable forms are also present in the coast of East Africa, islands of the Indian Ocean, Melanesia, China.

This differentiation in New Caledonia suggests the existence of a significant influence of the environment on certain characters of this species. Nevertheless, the above three forms cannot be considered as subspecies because of their geographical dispersion and the existence, even at the populational level, of many intermediate forms.

Fulvia (Fulvia) fragiformis sp. nov.
(pl. 3, figs. 2a-b)

Types:

The only known four shells, in MNHN, from New Caledonia. **Holotype**: Found alive near Abore reef (22°47' S-166°40' E), Depth 15m, H=16.5, L=15.7, W=11.2, with 52 ribs. Angle A =150°, ratio D= 1.4. (pl. 3, figs. 2a-b). **Paratype n° 1**: Dredged in the SE lagoon, sta.731 (21°17'2 S-165°52'0 E), depth 40m, H=12.1, L= 11.0, W= 9.0, with 49 ribs, **Paratype n° 2**: Dredged in the S lagoon, sta.589 (22°31'7 S-167°23'0 E), depth 31m H=11.1, L= 10.6, W=7.4, with 45 ribs. **Paratype No 3**: A left valve dredged in the SW lagoon, sta.21 (22°22'1 S-166°23'4 E), depth 16m, H=16.6, L=16.8, 1/2W=5.3, with 46 ribs.

Description:

Shell small, the paratype No 3 being the largest, thin and fragile.

Very special shape comparable to some FRAGINAE, with the PT in a different plane and separated by a rounded angle . This PT is largely reduced. In consequence of these particular features, the shell has an uncommon asymmetry, with the anterior half longer than the higher posterior half. Posterior groove present, well marked in the interior of the shell.

Lunule small, without perilunular furrow. Lunular heart very small. No trace of coloured sublunule. Last flat small, slightly concave. Last fold large, almost flat.

External colour white to yellowish, with more or less zigzagging irregular brown-purple concentric stripes. A brown spot on the umbo.

Internal colour similar by transparency.

Number of ribs 45 to 52. In the AT and the MT the ribs are mainly flat rounded and roughly equivalent in width between themselves, the interstices being a little wider than the ribs, particularly in the AT. In the PT1 the ribs and interstices are equivalent and wider, the ribs being rounded to flatly triangular. In the PT2 the ribs become more triangular with, in the smallest specimen, interstices wider and flat. In all specimens the IMR is very little marked in the PT2.

Periostracal insertions strong, situated on the posterior side of the ribs in the AT and MT, then on the middle of the triangular ribs in the PT, with the nodes sometimes a little calcified.

Granulation present, but not very abundant in the AT and sometimes in the PT.

Hinge thin with small teeth.

Ocular organs observed.

Material examined and distribution: The type material.

Habitat: Shallow water in clean non terrigenous facies.

Observations: *Fulvia fragiformis* is very close to *F. australis*, except for its very characteristic shape, never observed in the latter.There are also slight differences in the ribbing and the IMR (a little less marked), in the thicker periostracal lamellae, and in the stronger granules in *F. fragiformis*.

Fulvia (Fulvia) boholensis sp. nov.
(pl. 3, figs. 6a-b)

Types:

The type series in the MNHN. **Holotype**: from Panglao, Bohol Island, Philippines. It is said to have been recovered at 80 fms. Dimensions: H=36.0, L=35.2, W=21.6. Angle A=130°, ratio D=1.2, 55 ribs (pl.3 ,figs. 6a-b). **Paratype n° 1**: From Philippines, without precise data, H=33.5, L=34.0, W=21.1. Angle A=130°, ratio D=1.2, 54 ribs. **Paratype n° 2**: From Sulu Sea, Philippines. H=33.3, L=35.1, W=20.8. Angle A=130°, ratio D=1.1, 52 ribs. **Paratype n° 3**: From Philippines, without precise data, H=28.0, L=27.4, W=17.2. Angle A=130°, ratio D=1.2, 50 ribs.

Description:

Shell of medium size, up to 36 mm in length, relatively thin and fragile.

Always significantly asymmetric, obliquely expanded backwards, truncated in the PT2, rather depressed (mean W/L=0.62). Posterior groove well developed.

Lunule medium with a small lunular heart. Sublunule often present but always very short (like *F. australis*). Last flat medium. Last fold flatly triangular with no periostracal insertions.

Colour almost always orange or yellowish-orange internally and externally, the umbo and margins often being darker. The lighter medial zone of the shell often bears a little darker irregular concentric stripes. Some rare specimens (like paratype No 3) have "normal" colours: beige, light brown, purple, a part of the internal PT only being orange. The only observed specimen from outside of the Philippines (Western Australia) is yellow-orange with white margins.

Mean number of ribs 51 (range 47-55).

Ribs a little triangular in the AT, with wider interstices, flat or flatly rounded in the MT, with interstices about equivalent in width, slightly triangular with wider interstices in the PT2. IMR extending far from the margin, often not perfectly marked in the MT which has a thin and fragile margin.

Periostracal insertions of rather complex arrangement, situated on the posterior side or on the crest of the ribs. One of the radial components of these insertions become calcified and form, at each node, a thin oblique often elongated tubercle, in the PT.

Granules numerous in the anterior half of the shell, often aligned on short distances.

Ocular organs: no data.

Material examined and distribution: The type specimens and four corresponding lots- Other lots: PHILIPPINES: Bohol: 1 QM- AUSTRALIA: Western Australia, Dampier: 1 QM.

Observations: *Fulvia boholensis* seems to be an intermediate form between *F. australis* and *F. papyracea*. It differs from the former by its ribbing, particularly its IMR which is smoother, from the latter by its ribbing and its asymmetry. It differs from both by its particular colours, and also from all *Fulvia* by the particular arrangement of the periostracal insertions in the PT forming elongated carbonaceous tubercles. (The equivalent tubercles of *F. fragilis* are different and not elongated).

Fulvia (Fulvia) dulcis (Deshayes, 1863)
(pl. 1, fig. 8; pl. 2, figs. 8a-b)

Cardium dulce Deshayes, 1863: 12, pl. 29, figs. 3-5.

Types:

Four **syntypes** in the MNHN from Réunion, 12.0 to 7.1 mm in eight. The largest: H=12.0, L=11.5, W=8.7, with 41 ribs, is selected here as **lectotype** (pl. 2, figs. 8a-b).

Description:

Shell small, the above lectotype being the largest specimen observed.

Shell roughly equilateral, with the anterior margin rounded and the posterior one a little straightened. Almost circular, with L/H close to 1. Presence of a weak posterior groove corresponding inside to a well marked ridge.

Lunule of medium size, without perilunular furrow. Lunular heart rather large. Presence of a long sublunule, about equivalent in length to the lunule. Last flat small. Last fold very large, a little rounded to flatly triangular (pl. 1, fig. 8).

External colours: in the Indian Ocean the shells are whitish with a pink coloration in the umbo, diminishing towards the margin, forming a few irregular concentric stripes more or less zigzagging. The AT and PT zones are also light pink. Some specimens are entirely white.In the Pacific, same coloration but light brown instead of pink.

Interior with same colours by transparency.

Number of ribs: 41 to 47. The ribs of the AT and MT zones are equivalent in width with the interstices. They are flatly rounded, low, and hardly perceptible with the naked eyes, with no difference between these two zones. The IMR of the above zones is also regular, well perceptible, extending far from the margin which is also distinctly serrated. In the PT1 the ribs become suddenly wider and stronger, with equivalent interstices. They are also well marked, but smaller and more numerous, in the PT2 with possibly some intersticial riblets. In the lunule and sublunule, the growth lines form very thin concentric folds.

Periostracal insertions (3 to 5) without ribs in the sublunule. Present also in the AT and the MT and situated on the posterior limit of the ribs. The insertions migrate to the axial part of the ribs in the first ribs of the PT, then can disappear: in that case some ribs of the PT do not bear any insertion, or rudimentary ones.

Granules often numerous, but never aligned, on the posterior side of the shell, even on the posterior flat and fold (pl. 1, fig. 8); they are rarer on the anterior part. They can be totally absent from the whole shell.

Hinge with no particularities, with both sides almost symmetric.

Ocular organs observed.

Material examined and distribution: The type specimens- Other lots: SOUTH AFRICA: Zululand: 10 NM- PAPUA: Hansa Bay: 1 QM- NEW CALEDONIA: 33 MNHN.

Habitat: In Réunion, according to DRIVAS & JAY (1988: 16), it is "found alive in muddy black sand at 12 to 30 m depth".

In New Caledonia also it is exclusively present in shallow terrigenous facies, East of the island, between 20 and 50m. In South Africa it was dredged in fine sandy facies between 45 and 50 m depth.

Observations: *F. dulcis* is easily distinguished from several small forms of *Fulvia* by its periostracal insertions, and from the young specimens of *F. australis* by its more equilateral and globular shape and by its longer sublunule.

Fulvia (Fulvia) scalata sp. nov.
(pl. 1, figs.3 and 4; pl. 3,figs. 5a-b and 7)

Types:

Types from the eastern lagoon of New Caledonia. **Holotype**: In the MNHN, sta.833 (20° 27'6- 164° 44'3), depth 27m, H=19.1, L=19.3, W=14.8, with 46 ribs, (pl.3, figs. 5a-b). **Paratype n° 1**: In the MNHN, same sta. as holotype, H=17.6, L=18.4, W=12.7, with 43 ribs. **Paratype n° 2**: In the MNHN, sta.883 (20°27'6 S-164°44'3 E), depth 27m, H=17.1, L=17.2, W=12.4, with 42 ribs. **Paratype n° 3**: In the MNHN, sta.873 (20°38'55 S-164°46'2 E), depth 27m, H=15.0, L=15.2, W=11.5, with 37 ribs. **Paratype n° 4**: In the MNHN, sta.847 (20°37'65 S-165°13'4 E), depth 28m, H=11.0, L=11.1, W=8.3, with 38 ribs. **Paratype n° 5**: In the AMS, same sta. as holotype, H=16.6, L=16.8, W=11.1, with 48 ribs. **Paratype n° 6**: In the ANSP, same sta., H=17.7, L=17.8, W=13.0), with 51 ribs. **Paratype n° 7**: In the NMNZ, same sta., H=17.3, L=16.7, W=12.7, with 45 ribs.

Description:

Shell small, the holotype being the largest specimen observed.

Roughly equilateral, with the anterior margin rounded and the posterior one a little straightened. Almost circular, with L/H very close to 1.0. Presence of a very weak posterior groove, only in adult shells.

Lunule rather small, without perilunular furrow. Lunular heart extremely large, the largest of all the *Fulvia* (pl. 1, fig. 3). Presence of a sublunule of rather variable length, but never as long as the lunule (varying between 1/2 and 3/4 of the lunule), with no periostracal insertions but sometimes with a rudimentary rib in its middle. Last flat extremely large, sometimes divided into two differently tilted zones. Last fold also extremely large with a posterior triangular part and a flat large anterior one.

External colour generally white to light brown, rarely with concentric irregular darker stripes. Umbo and posterior part often darker coloured.

Internally, the umbonal cavity is often yellow to pinkish and the posterior part slightly purple.

Number of ribs about 40 (range 36-44). With the exception of the PT2, the ribs are strictly equivalent in width to the interstices. The ribs, well rounded in the AT, then becoming more or less flatly rounded or flat in the MT, are well delimited, contrasting with the

flat interstices. The ribs are weaker in the MT but always well perceptible in the adult shells. In the PT1 the ribs and interstices are a little wider and stronger than in the other parts of the shell. In the PT2 the interstices are very narrow, the two last ribs being very large and flat, and the others narrow and a little triangular. The IMR is very well marked and extended. In the lunule and sublunule, the growth lines form thin concentric folds.

Periostracal insertions situated on the posterior limit of the ribs in the AT and MT, then migrating progressively to the top of the ribs in the PT.

Granulation almost always present both in the anterior half, including the lunule, and in the posterior half, including the last flat and fold. In the AT and PT1, the granules are located in the interstices, aligned and placed at more or less regular intervals, like rungs in a ladder (scalata). In the very young shells, granulation can also be developped in the MT, forming irregular concentric lines (pl. 1, figs. 4 and pl. 3, fig. 7).

Hinge typical of the genus, very asymmetric as far as laterals are concerned (D= 1.7 to 1.8), with a particular triangular nymph strongly projecting exteriorly beyond the margin of the shell.

Ocular organs observed.

Material examined and distribution: The type series- other lots: OMAN: Mascate : 1 MNHN- MADAGASCAR: Tulear: 4 MNHN- PHILIPPINES: Visayas and Luzon: 2 MNHN, 1 WAM- INDONESIA: Macassar Strait: 1 MNHN; Moluccas 1 WAM- PAPUA: Hansa Bay: 3 IRSNB- NEW CALEDONIA: 75 MNHN- AUSTRALIA: Queensland: 7 AMS; Carpentaria: 1 QM; Western Australia: Dampier: 1 QM; i WAM.

Habitat: In New Caledonia only found in shallow water from 20 to 50 m (never littoral), and in the terrigenous sandy facies of the Eastern coast (rarely in clean perireefal facies).

Fulvia (Laevifulvia) undatopicta (Pilsbry, 1904)

(pl.1, figs.1 and 2; pl. 2, figs.9a-b, 10 and 11)

Cardium hungerfordi undatopictum Pilsbry, 1904: 556, pl. 40, figs. 14-15.
Cardium undatopictum Pilsbry: Nomura & Niino, 1940: 55.

Synomym:
Cardium hungerfordi stigmaticum Pilsbry, 1904: 556, pl. 41, figs. 13-14.

Types:

Cardium hungerfordi undatopictum: **Syntypes** in the ANSP, reg. n° 80521: from Hirado, Hizen, Japan (Hirase collection, 1901), four paired specimens and one right valve, from 11.6 to 18.3 mm in height. The largest (H=18.3, L=17.5, W=10.5), with 48 ribs, is figured by Pilsbry and here in pl. 2, figs. 9a-b.

Cardium hungerfordi stigmaticum: **Syntypes** in the ANSP, reg. n° 86.279: also from Hirado, Hizen, Japan, three paired specimens from 10.5 to 11.7 mm in height. The largest (H=11.7, L= 11.0, W= 7.5) is figured by Pilsbry and here in pl. 2, fig. 11.

Description:

Shell small. The first syntype above cited being the largest observed.

Generally roughly equilateral, rarely appreciably obliquely inequilateral (like some syntypes). Often slightly truncated posteriorly, sometimes with a small open indentation in the margin corresponding with the posterior groove which is more or less developed. Shell a little higher than long: L/H range 0.88-0.93.

Lunule of medium size with a rather small lunular heart (pl. 1, fig 2), both not coloured. Sublunule long, length equal to the lunule (pl. 1, fig. 1).

External colour very variable from pure white to almost entirely dark brown purple. Often whitish to beige with more or less developed irregular brown red stripes or zigzags. Sometimes only coloured by small spots. Four different red stains can be present, often together, forming a cross: one stain on the umbo, another one radially elongated in the middle of the shell (the variety *stigmaticum* of Pilsbry is a pure white form with only these two stains, see pl. 2, fig. 11), a third one on the sublunule, and the last one on the posterior margin on the PT2 zone. In the syntypes of undatopicta, these stains are not present, or extremely pale.

The internal colours are the same, by transparency.

Mean number of ribs about 48 (range 46-53), with 10 in the PT. From the medio-posterior part of the MT, where the ribs are present but not easily discernible, they become progressively a little more developed and wider towards the AT where, however, they remain of moderate development. Towards the PT, the ribs evolve in the same way, but they become quickly well marked and wider in this zone.They are generally flatly rounded, except in the PT2 where they become somewhat triangular, and equivalent in width with the

interstices. The IMR is always clearly discernible and shows the same evolutions as the external ribbing. Intersticial riblets present in the PT2, where the ribs tend to be very wide close to the posterior margin. In the sublunule and the posterior part of the lunule, the growth lines tend to form thin concentric folds.

No periostracal insertions.

Granules more or less abundant, but always present, concentrically aligned on long distances in the AT (pl. 2, fig. 10), rare to absent in the MT, more or less abundant and not aligned in the PT.

Hinge characteristic of the genus, regularly curved. Nymphal plate narrow, not triangular.

Ocular organs observed.

Material examined and distribution: The type material- Other lots: Red Sea: 4 MNHN- EGYPT: Gulf of Suez: 2 MNHN- DJIBOUTI: 1 MNHN- YEMEN: Aden: 1 MNHN- MADAGASCAR: Dredging Tulear: 8 MNHN; Nosy Bé,: 1 MNHN- THAILAND: Kut Is: 1 AMS- PHILIPPINES: Visayas: 1 MNHN- JAPAN: Tosa: 1 MNHN- PAPUA: Hansa Bay: 1 IRSNB; 1 QM- NEW CALEDONIA: 232 MNHN - AUSTRALIA: Queensland: 5 AMS; Gulf of Carpentaria: 1 AMS.

Habitat: Only shallow water, rarely littoral. In New Caledonia, lives in reefal or perireefal calcareous facies, between 10 and 35m.

Fulvia (Laevifulvia) lineonotata sp. nov.
(pl. 3, figs.4a-b)

Types:

Types from New Caledonia. **Holotype**: In MNHN, sta.992 (20°16'1 S-163°56'6 E), depth 28 m, H=13.6, L=11.1, W=8.2, with 52 ribs (pl. 3, figs. 4a-b). **Paratype n° 1**: In MNHN, same sta. as holotype, H=8.9, L= 8.0, W= 5.2. **Paratype n° 2**: In MNHN, Chesterfield lagoon sta.DW 31 (19°24'86 S-158°45'03 E), depth 57m, H=10.2, L= 9.6, W=6.3. **Paratype n° 3** in MNHN, Chesterfield lagoon sta DW 50 (19°18'30 S-158°33'57 E), depth 50m, H=10.2, L=9.6, W=6.1. **Paratype n° 4**: In MNHN, Chesterfield lagoon sta.DW40 (19°29'46 S-158°35'27 E), depth 58m, H= 9.7, L=8.7, W=6.0. **Paratype n° 5**: In AMS, sta.1174 (19°21'3 S-163°14'2 E), depth 53m, H=10.2, L=9.2, W=6.1. **Paratype n° 6**: In ANSP, same sta. as holotype, H=9.0, L=8.2, W=5.3. **Paratype n° 7**: In NMNZ, sta.542 (19°06'4 S-163°10'0 E), depth 5Om, H=10.0, L=9.1, W=6.0.

Description:

Shell small about 10mm in height, the holotype of 13.6 mm being the largest observed.

Always a little elongated (L/H between 0.84 and 0.94). Asymmetric with the anterior margin rounded and the posterior margin a little obliquely expanded, with a small depression at the extremity of the posterior groove, which is weakly but always developed.

Lunule rather small without lunular heart and with no or very small perilunular furrow, limited by a coloured line formed by triangular spots. Presence of a very long sublunule (1.5 times or more the lunule), the longest of all the *Fulvia*.

External coloration constituted by juxtaposed or imbricated differently coloured (white to brown purple) triangles, with more or less diffuse limits. The posterior part of the MT is marked by a radial alignment of darker coloured triangles , alternating with white ones. This coloured "line", almost always perceptible, gave its name to the species. Umbo and often posterior margin stained red purple.

Internal coloration the same as the external one by transparency.

Ribs almost indiscernible in the AT and MT, but the IMR, limited to a small band, is clearly discernible and allows counting of about 40 ribs in these two zones. The PT bears about 13-15 well marked ribs, flatly triangular, with narrow interstices. The narrowest ribs (about four in number) are located in the anterior part of the PT2. These ribs are often poorly marked and can disappear. Except in the PT, the growth lines form very thin concentric folds.

No periostracal insertions.

Thin granules, often concentrically aligned, on all the anterior half of the shell including the lunule.

Hinge very thin, particularly the nymphal plate, and well arced. Angle A of medium value for the genus, and ratio D higher than 1.0.

Ocular organs observed.

Material examined and distribution: The type material- Other lots: MAURITIUS: Port Louis: 1 NM- INDIA: Maldives, Milandu Atoll: 1 BM(NH)- NEW CALEDONIA: 45 MNHN.

Habitat: in New Caledonia exclusively shallow water, in clean calcareous facies from 25 to 60m.

Observations: *Fulvia lineonotata* is easily separated from the other small *Laevifulvia* by its elongated oblique shape, its particular colour pattern, its long sublunule.

Some small specimens of *Laevicardium lobulatum* Deshayes, 1855, which are sometimes sympatric in New Caledonia, can have approximately the same shape and colours, and easily be confused. Nevertheless, the latter has still less perceptible ribs in the AT and MT and no ribs in the PT2, many more "ribs" in the IMR (about 85 versus 55), a shorter sublunule and no granules. In addition the umbo of this species bears a special reticulated ornamentation, never observed in any *Fulvia*, and it never has ocular organs.

Fulvia (Laevifulvia) hungerfordi Sowerby, 1901 (pl. 2, figs. 12a-b, 13, 14 and 15)

Cardium (Papyridia) hungerfordi Sowerby, 1901: 103, pl. 9 fig 5.

Types:

Three **syntypes** from Japan, preserved in the BM(NH), reg. 1902.5.28.5.7, respectively 9.0, 8.4 and 8.0 mm in length.
The two latter are figured here pl. 2, figs. 12a and 12b.

Description:

Shell small up to 14 mm in length.

Always longer than high (L/H range 1.02 to 1.16). Generally inequilateral with the posterior part expanded, but never obliquely; nevertheless Indonesian forms are quasi-perfectly equilateral. Posterior margin a little truncated in the PT2, and PT1 often lengthened, overstepping a little the margin of the shell; some slight straightenings in the ventral and anterior margins can give the shell like a vague "polygonal" aspect, with a sharpening in the posterior margin. Posterior groove weak but well marked in the early stage of growth, disappearing in the adult shell.

Lunule medium, flat or a little concave, limited by a significant rounded ridge, clearly delineated also in the early stage of growth. Lunular heart small. Sublunule of variable length, according to the different populations (between one half and almost one and a half times the length of the lunule). Last flat large, a little concave. Last fold large, flatly triangular.

Colour of the shells, external and internal, uniform, from beige to brown or red purple, becoming lighter towards the margins.

About 10 ribs in the AT, 12 ribs in the PT and 20-22 ribs in the MT when this third is ribbed. The ribs are generally equal in width with the interstices, except in the PT2 where the interstices are very thin. In the AT the ribs have a rounded or slightly flatly rounded profile and the interstices are flat. In the PT1 the ribs and the interstices, the largest of all the shell, both have a rounded profile. In the PT2 the ribs flatten. As far as the the MT is concerned, it can be entirely ribbed like the AT, or partially ribbed, or not ribbed, according to populations (see later).In all the forms, the growth lines form, in the adult shells, more or less strong concentric folds, except in the PT.

No periostracal insertions.

Granulation of variable density (sometimes absent) on the whole shell, sometimes perfectly concentrically aligned in the MT.

Hinge with no particularities.

Siphonal eyes present according to Reid & Shin, 1983: 277, fig. 1.

Material examined, distribution and observations : Observed specimens from four areas:

Japan: Syntypes and specimens of the ANSP cited by Pilsbry (1904: 555, pl. 41, fig. 17). Inequilateral forms with no ribbing in the MT. Found in littoral and shallow water in organic muddy facies. Recorded also from Hong Kong (Reid & Shin, 1983: 275), but with no data about the shell itself.

Philippines: One lot from Musorstom Campaign 1985, sta. DR 140, Jintololo channel, North of Panay Island, depth 93-99m in clean muddy and shelly facies (thanatocenosis). Inequilateral forms with partial variable development of ribs in the MT (pl. 2, fig. 13).

Indonesia: Two lots from Siboga Expedition: sta.53, North of Sumba Island, depth 36m in coral sand and sta.174, East of Ceram Island, in very shallow reef facies. In both areas the shells are almost equilateral with ribs in the MT (pl. 2, fig. 14).

New Caledonia: Only in one locality: Gatope Beach, near Voh, in the North-Western coast, littoral in deltaic argillaceous sandy facies. Asymmetric forms with ribs in the MT (pl. 2, fig. 15).

Fulvia (Laevifulvia) prashadi sp. nov. (pl. 3, figs. 8a-b)

Types:

In the ZMA, from Siboga expedition, sta.71, South of Macassar Strait, Indonesia, depth 32m, in mud, sand with mud and coral. Identified as *Cardium hungerfordi* Sow by Prashad (1932: 281). **Holotype**: A right valve H=10.2, L=10.2, 1/2W=0.4 (pl.3, figs. 8a-b). **Paratype n° 1-** A left valve H=9.3, L=9.3,

1/2W=0.37. **Paratype n° 2-** A right valve H= 9.0, L=9.0, 1/2W=0.35. **Paratype n° 3-** A left valve H=7.5, L=7.7, 1/2W=0.3.

Description:

Shell small, the holotype being the largest known specimen.

Shape relatively constant, inequilateral, with the anterior side short and slightly truncated and the posterior one not obliquely expanded. Often the MT margin is straightened in its posterior part. The PT is sharpened and clearly isolated from the rest of the shell by a significant notch in the margin, the PT forming a ridge making the margin pointed.

Lunule medium, a little concave, limited by a rounded ridge well delineated, even in the earliest stage of growth. Lunular heart small. Sublunule equivalent to the lunule in length, or a little longer. Last flat large, a little concave. Last fold large, flatly triangular.

External colour uniformly light beige. Internally yellow, lighter in the axis of the umbonal cavity, with the posterior part a little purplish.

About ten ribs in the AT equivalent in width to the interstices, with a well marked IMR. No ribs nor IMR in the MT.

About ten strong ribs in the PT, equivalent in width to the interstices in the PT1, wider in the PT2, corresponding to a strong IMR. In the whole shell, presence of well marked rounded concentric folds, corresponding to the growth stages.

No periostracal insertions.

Never seen any granulation on the few specimens observed.

Hinge with no particularities.

Ocular organs: no data.

Material examined and distribution: Found only by the Siboga expedition in Indonesia in five stations: sta. 71, South of Macassar Strait near Sulawesi coast: eleven valves (type series) sta.4, East Java, depth 9m in coarse sand: 1 specimen and one valve - sta.33, East Lombok Island, depth 22m in mud, coral and coral sand: one specimen - sta.164, South of Salawati Island, North East New Guinea, depth 32m in mud, sand and coral: one specimen - sta.114, North coast of Sulawesi, depth 75m in very fine hard sand: one specimen.

Observations: *Fulvia prashadi* is close to certain forms of *F. hungerfordi* and could be considered as a special form or a subspecies of the latter. The problem needs more material to be solved. In favour of a specific separation is the fact that the only two known sites of *F. hungerfordi* in Indonesia (Siboga sta. 53 and 174) are close to sites of the former, and contain quite different symmetrical specimens (pl. 2, fig. 14), constant in characters. It is the same for *F. prashadi* which shows very constant characters in the five sites where it is found in Indonesia. Anyway, I think that these very special forms merit a new name (species or subspecies).

Fulvia (Laevifulvia) ballieni sp. nov.
(pl. 3, figs. 3a-b)

Type:

Holotype in the MNHN labelled "Sandwich Islands, Mr Ballien 1876". It may seem improbable that such a large and remarkable Hawaiian bivalve has remained unknown to this date. Indeed, that it is known from a single shell, collected in the 19th century, in a European Museum, is suspect. No *Fulvia* or *Laevicardium* is known from Hawaii, and there is no material in the Bishop Museum (Kraslowitz, pers. comm.). I cannot exclude the possibility that the shell of *F. ballieni* has been erroneously labelled and in fact it does not originates from Hawaii. However, there are indications in the catalogue of the MNHN that a Mr Ballien did send repeatedly shells from Honolulu between 1872 and 1878. *Fulvia ballieni*, be it Hawaiian or not, must be a rare species, as evidenced by the fact that no other specimen has shown up since Ballien's collect in 1876.

Description:

Shell of medium size: H = 48.0, L = 49.3, W = 34.3.

Practically equilateral, but with a very small double-truncation making the PT slightly sharpened. No gaping.

Lunule not separated from the sublunule, which is a little shorter than the lunule. Lunular heart very small. Last flat hardly differentiated, a little concave. Last fold narrow, triangular.

External colour uniformly light beige, shining. Interior whitish, with the margin yellowish.

Number of ribs 50. The ribs and interstices are hardly marked on the whole shell, a little more in the PT1. No ribs in the PT2 which is smooth, externally and internally. The IMR, which extends rather far from the margin, is very better marked than the ribbing and shows "ribs" a little narrower than "interstices".

No periostracal insertions.

Granules more or less aligned present only on the umbonal part up to about one centimetre from the umbo.

Hinge typical of the genus. Angle A = 130°. Ratio D = 1.32.

Ocular organs: no data.

Material examined and distribution: Only the holotype, maybe from Hawaii.

Observations: Shining apart, *Fulvia ballieni* has approximately the same appearence as *F. mutica* from which it differs by many other characters (no periostracal insertions, rather long sublunule, etc...). It differs mainly from the other species of the subgenus *Laevifulvia* by the size, the homogeneity of the ribbing and IMR in the AT and MT, by the presence of a smooth PT2. Because of this latter character it approaches the genus *Laevicardium* (convergence).

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PLATE 1 (opposite page):

Fig.1 - *Fulvia undatopicta*, NC SE lagoon sta.703. MNHN. Real L=9.4mm.
Fig.2 - *Fulvia undatopicta*, lunular heart, NC NW lagoon sta.992. MNHN. Scale: x14.
Fig.3 - *Fulvia scalata*, lunular heart, NC N lagoon sta.1063. MNHN. Scale: x14.
Fig.4 - *Fulvia scalata*, N Qld 15°45-145°35, AMS C44644. Real L=3.0mm.
Fig.5 - *Fulvia mutica*, periostracal insertions in the PT. Japan. MNHN. Scale: x45.
Fig.6 - *Fulvia fragilis*, periostracal insertions in the PT. Aden. MNHN. Scale: x55.
Fig.7 - *Fulvia papyracea*, periostracal insertions in the MT. Subic Bay Philippines. MNHN. Scale: x150.
Fig.8 - *Fulvia dulcis*, posterior part. NC SE lagoon sta.688. MNHN. Scale: x13.
Fig.9a-b - Selected lectotype of *Cardium apertum* Brug. and *C. hians* Spengler. Real L=48.1mm.
Fig.10a-b - Holotype of *Fulvia voskuili*. Real L=33.8mm.
Fig.11a-b - Holotype of *Cardium papyraceum*. Real L=37.4mm.
Fig.12a-b - Syntype of *Cardium annae* figured by Pilsbry. Real L=27.2mm.

PL1

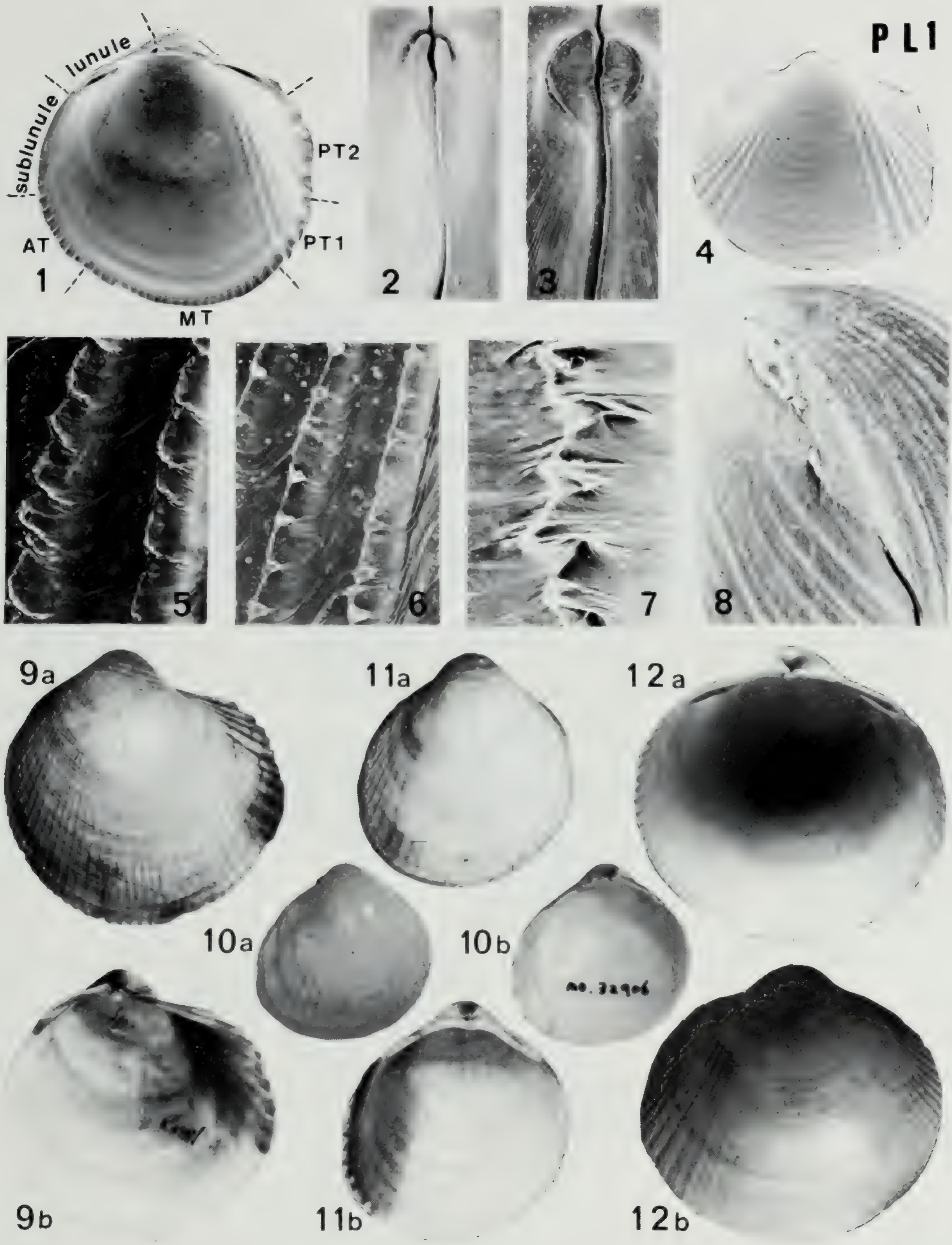
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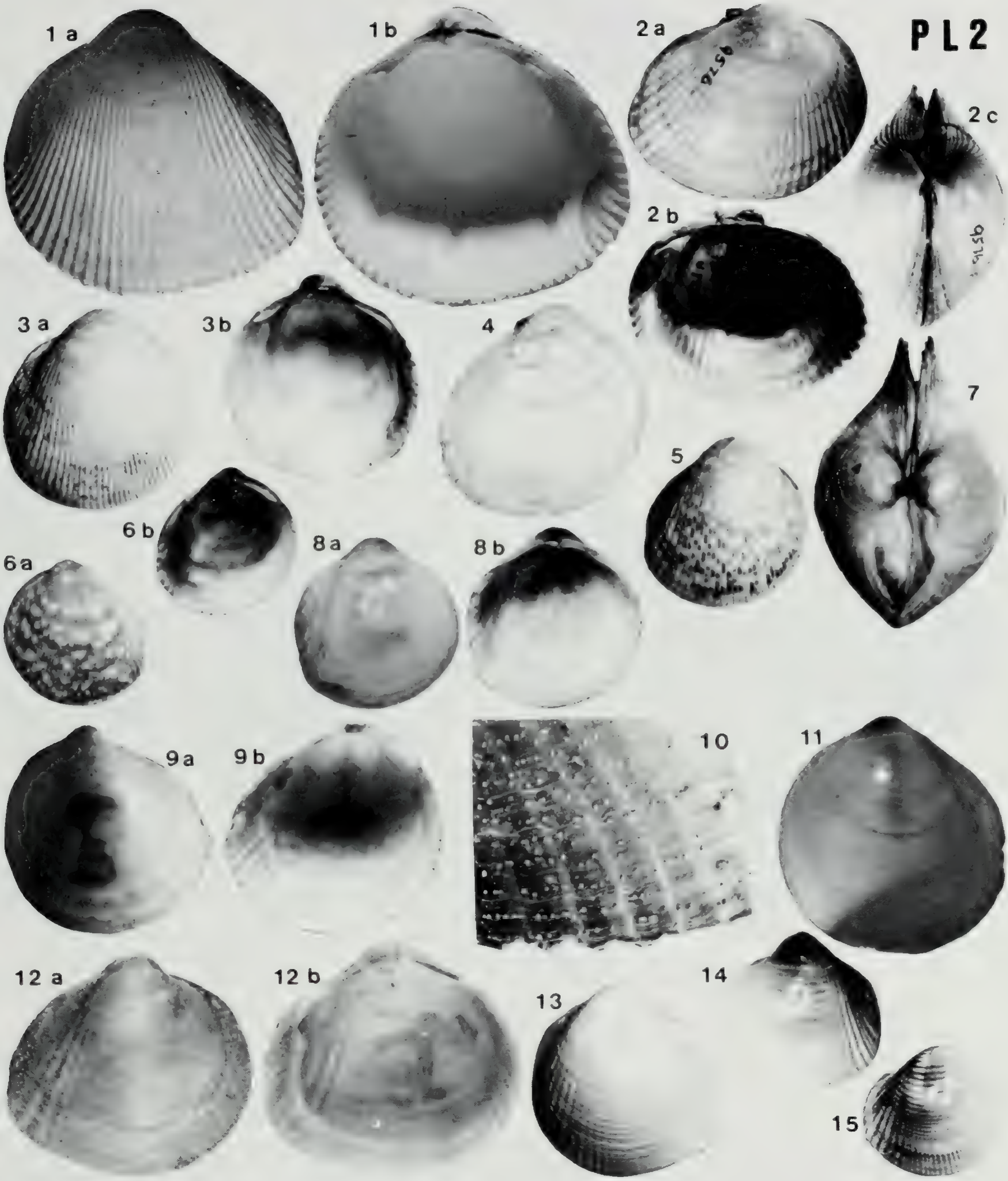
PLATE 2 (opposite page):

Fig.1a-b - Selected lectotype of *Cardium tenuicostatum*. Real L=54.0mm.
Fig.2a-b - *Fulvia natalensis*, Port Elizabeth SA, NM 5776. Real L=39.0mm.
Fig.2c - *Fulvia natalensis*, Port Elizabeth SA, NM 5776. Real L=37.4mm.
Fig.3a-b - *Fulvia australis*, NC S lagoon sta.557, depth 44m. MNHN. Real L=31.9mm.
Fig.4 - *Fulvia australis*, N Qld Fantome Is, QM mo 45527. Real L=34.6mm.
Fig.5 - *Fulvia australis*, NC Nouméa, MNHN. Real L=27.1mm.
Fig.6a-b - *Fulvia australis*, N Qld Shelburne Bay, QM mo 45517. Real L=24.8 mm.
Fig.7 - Selected lectotype of *Cardium apertum*. (See pl.1, fig.9a-b).
Fig.8a-b - Selected lectotype of *Cardium dulce*. Real L=11.5mm.
Fig.9a-b - *Cardium hungerfordi undatopictum*, syntype figured by Pilsbry. Real L=17.5mm.
Fig.10 - *Fulvia undatopicta*, detail of the AT, NC SE lagoon sta. 703, MNHN. Scale: x22.
Fig.11 - *Cardium hungerfordi stigmaticum*, syntype figured by Pilsbry. Real L=11.03 mm.
Fig,.12a-b - Two syntypes of *Cardium hungerfordi*. Real L respectively 8.0 and 8.4mm.
Fig.13 - *Fulvia hungerfordi*, Philippines N of Panay Is., sta. DR 140, MNHN. Real L=13.6mm.
Fig.14 - *Fulvia hungerfordi*, Indonesia N Sumba Is. ZMA. Real L=12.4mm.
Fig.15 - *Fulvia hungerfordi*, NC Gatope Beach, MNHN. Real L=9.0mm.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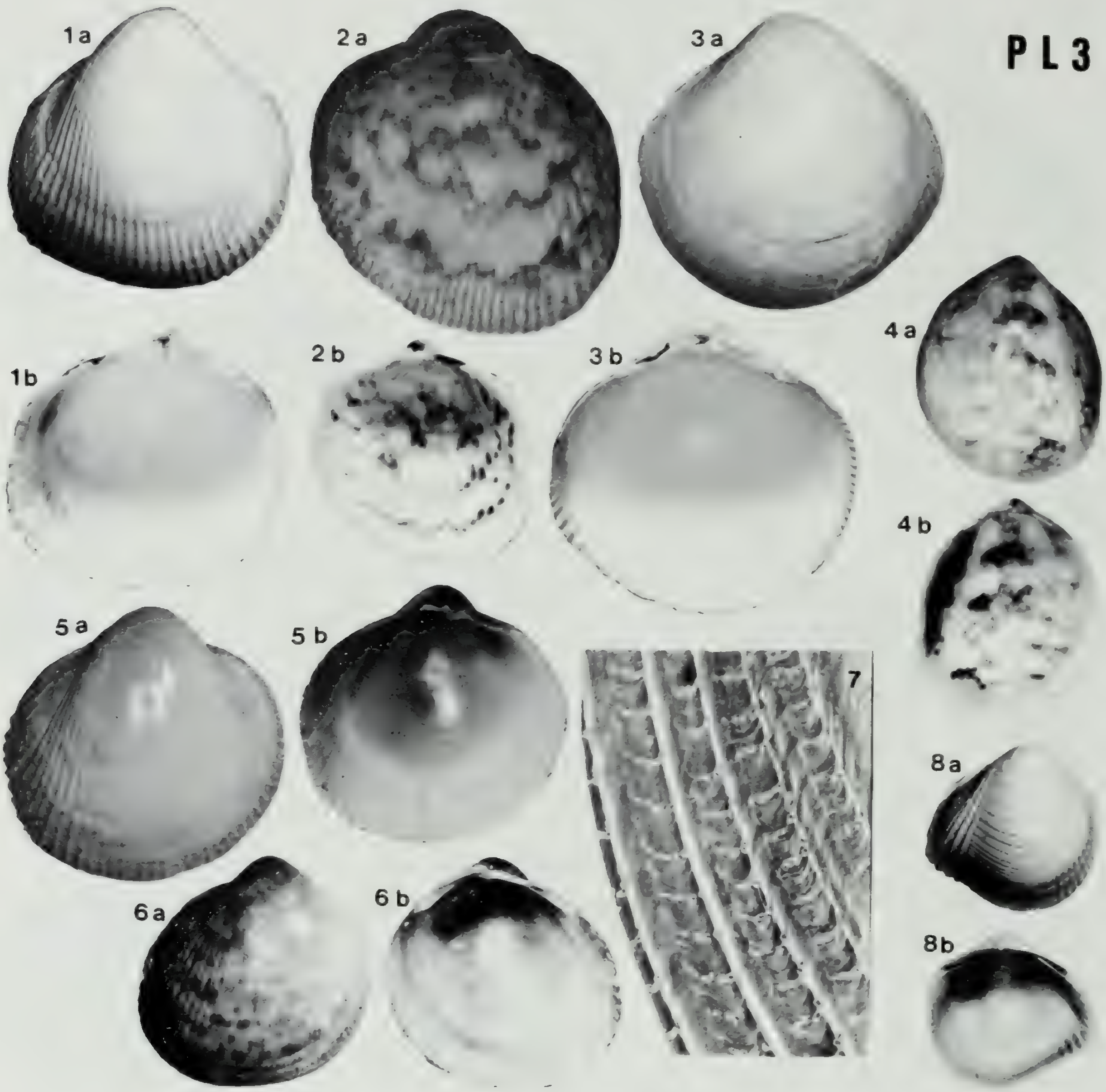

PLATE 3:
Fig.1a-b - *Fulvia fragilis*, Zanzibar, MNHN. Real L=45.3.
Fig.2a-b - Holotype of *Fulvia fragiformis*. Real L=11.0mm.
Fig.3a-b - Holotype of *Fulvia ballieni*. Real L=49.3mm.
Fig.4a-b - Holotype of *Fulvia lineonotata*. Real L=10.2mm.
Fig.5a-b - Holotype of *Fulvia scalata*. Real L=19.3mm.
Fig.6a-b - Holotype of *Fulvia boholensis*. Real L=35.2mm.
Fig.7 - *Fulvia scalata*, detail of the AT, NC NE lagoon sta. 846, MNHN. Scale: x25.
Fig.8a-b - Holotype of *Fulvia prashadi*. Real L=10.2mm.

The Muricidae (Gastropoda) from Madeira with the description of a new species of *Ocenebra* (*Ocinebrina*) (Muricidae: Ocenebrinae).

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KEYWORDS: Gastropoda, Muricidae, review, new species, Madeira.

ABSTRACT. Nine species of Muricidae are reported here from the Archipelago of Madeira (*Hexaplex trunculus, Ocenebra erinaceus, O. edwardsi, O. aciculata, O. inordinata* n.sp., *Bedeva paivae, Muricopsis aradasii, Cytharomorula grayi, and Stramonita haemastoma*). Two of these species, *Hexaplex trunculus* and *Bedeva paivae*, are new records for the Archipelago. Three species listed by previous authors remain doubtful records for the region and have not been confirmed [*Muricopsis cristatus, Orania fusulus*, and *Trophonopsis richardi* (= *T. droueti* or *T. muricatus*)]. The presence of *Typhis fistulatus* (= *Typhis sowerbyi*), once recorded from the Archipelago, is probably based on a misidentification, and is not accepted here. A new species, *Ocenebra (Ocinebrina) inordinata*, is described from the Island of Madeira.

RESUME. Neuf espèces de Muricidae sont signalées dans l'Archipel de Madère (*Hexaplex trunculus, Ocenebra erinaceus, O. edwardsi, O. aciculata, O. inordinata* n.sp., *Bedeva paivae, Muricopsis aradasii, Cytharomorula grayi,* et *Stramonita haemastoma*). Deux de ces espèces, *H. trunculus* et *B. paivae* sont signalées pour la première fois dans la région. Trois espèces listées par des auteurs précédents n'ont pas été retrouvées, leur présence dans l'Archipel reste douteuse [*Muricopsis cristatus, Orania fusulus,* et *Trophonopsis richardi* (= *T. droueti* ou *T. muricatus*)]. La présence de *Typhis fistulatus* (= *T. sowerbyi*), signalée précédemment dans l'Archipel est probablement basée sur mauvaise identification de l'espèce et n'est pas acceptée ici. Une nouvelle espèce, *Ocenebra (Ocinebrina) inordinata* est décrite de l'Ile de Madère.

INTRODUCTION

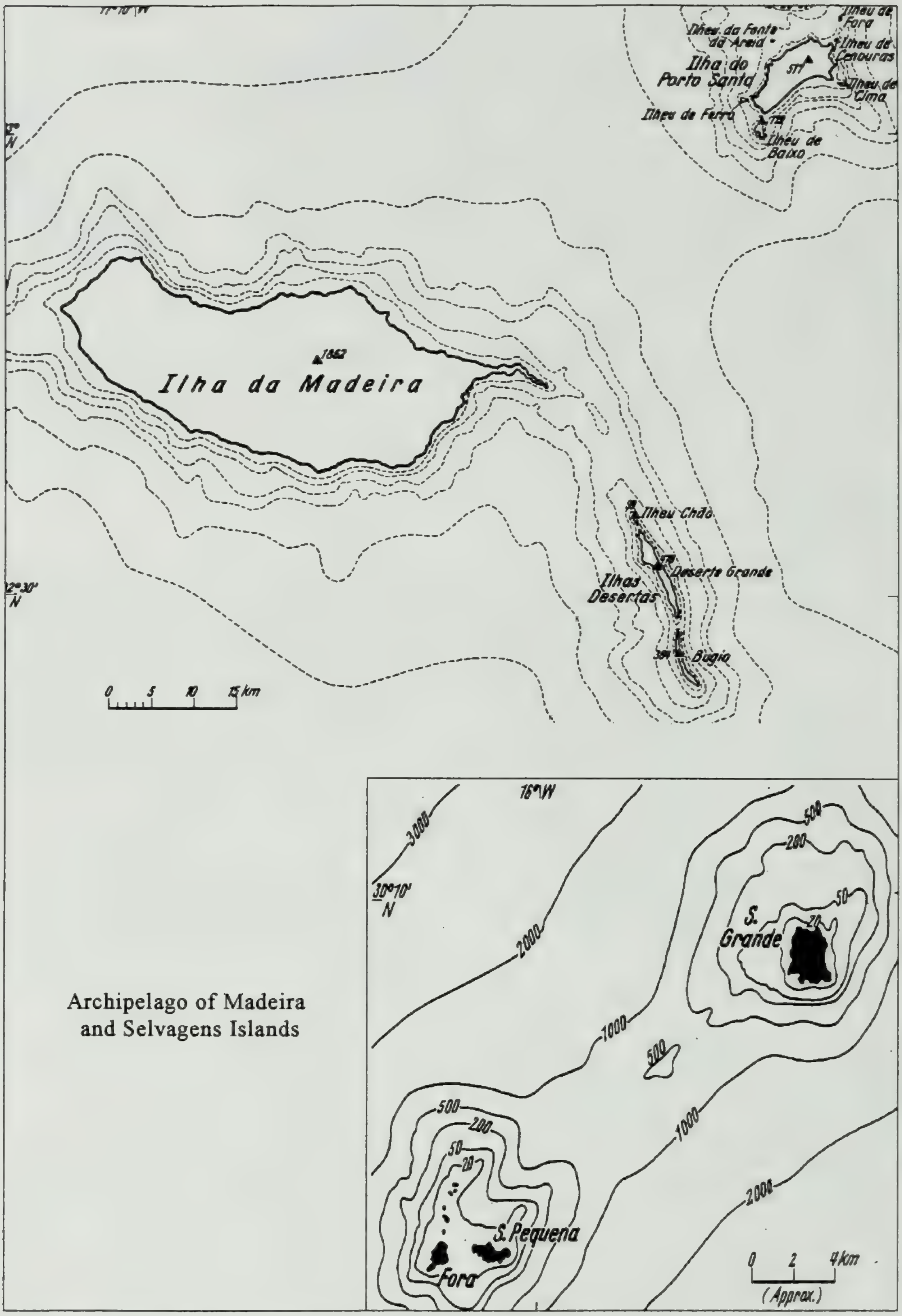
The Archipelago of Madeira is situated between 35°05' - 32°25' N and 17°15' - 16°15' W. It includes Madeira, Porto Santo, the Desertas and a group of islets around these islands. Administratively, the Selvagens Islands, situated 160 miles south of Madeira, between 30°12' - 30°02' N and 16°05' - 15°50' W, also belong to the madeiran archipelago.

The largest island of the archipelago is Madeira, which comprises an area of 737 km^2 and is situated 700 km off the coast of Morocco. Porto Santo is situated 20 miles NE of Madeira and its area is approximately 41 km^2 including the islets. The Desertas are composed of the Ilhéu Chão, Deserta Grande and the Bugio, which are situated 10 miles SE off Madeira and have an area of approximately 14 km^2. The Selvagens have an area of 4 km^2 (Text Fig. 1).

Despite small local and seasonal variations, the Archipelago of Madeira is strongly influenced by a current which flows from NE and is formed by a terminal branch of the Gulf Stream.

The mean temperature at the surface of the water in Madeira is 19.5° C. The lowest is 17.0° C (February and March) and the highest is 22.5° C in September. In the Selvagens the mean values are 0.3° C higher.

Faunal elements of several provinces are represented in the composition of the marine Mollusca of Madeira. There are species from North Africa, Western Mediterranean, NW and NE Atlantic, but also several dozen endemic species. From the biogeographic point of view, the Archipelago of Madeira is a part of Macaronesia which also includes the Azores, the Canary Islands and the Cape Verde Archipelago.



(Adapted from Michel-Thomé, 1976 - Geology of the Middle Atlantic Island)

The actual known total of the marine molluscan fauna of Madeira is about 500 species. The first author giving a general view of this matter was WATSON (1897) with a list containing 382 species. Later, NOBRE (1937) added 13 species to Watson's list. Apart from these two authors, NORDSIECK & TALAVERA (1979) have made a general study which, however, was only devoted to the Gastropoda. More recently, MOOLENBEEK & FABER (1987 a-c) and MOOLENBEEK & HOENSELAAR (1989) have dedicated special attention to the Rissoidae, describing some new species.

The family Muricidae in Madeira is represented by several species, but not all the species reported by previous authors were rediscovered by us. Of course, it does not mean *ipso facto* that these do not occur in Madeira at all, and later reports perhaps will confirm the presence of these in the Archipelago.

Abbreviatons

BMNH: The Natural History Museum, London.
MMF: Museu Municipal do Funchal, Madeira.
RH: Roland Houart collection.

SYSTEMATICS

Family MURICIDAE Rafinesque, 1815
Subfamily Muricinae Rafinesque, 1815
Genus *Hexaplex* Perry, 1811

Hexaplex trunculus (Linné, 1758)
Figs 1-2

Murex trunculus Linné, 1758: 747.

Records: Madeira (Garajau); Porto Santo; Desertas Is, many live and dead taken specimens at a depth of approximately 70 m. (MMF).

Remarks: *Hexaplex trunculus* is a very common species occuring in the Mediterranean Sea. The species was not reported before from the Madeira Archipelago, despite the fact that it is very common in Madeira and the other islands.

There are at least 40 synonyms known for this variable species, most of them named to designate minor morphological differences in shell structure such as the length of spines, the dimensions, the colour, etc.

Subfamily MURICOPSINAE
Radwin & D'Attilio, 1971
Genus *Muricopsis*
Bucquoy & Dautzenberg, 1882

Subgenus *Muricopsis*

Muricopsis (Muricopsis) cristatus
(Brocchi, 1814)

Murex cristatus Brocchi, 1814: 394, pl.7, fig.15.

Records: NOBRE, 1937: Funchal.

Remarks: As noted above, Muricopsis cristatus was listed in NOBRE (1937), but it is not yet recorded by us from the Archipelago. Its presence in Madeira, even if doubtful, is possible. The species is common in the Mediterranean Sea.

Subgenus *Murexsul* Iredale, 1915

Muricopsis (Murexsul) aradasii
(Monterosato, 1883)
Figs 3-4

Murex aradasii Monterosato in Poirier, 1883: 123.

Murex (Ocinebra) medicago Watson, 1897: 242, pl. 19, fig. 11.
Murex medicago -NOBRE, 1937: 29
Muricopsis medicago -NORDSIECK & GARCIA-TALAVERA: 131.

Records: Only a few specimens from Madeira (Caniçal) and Porto Santo (MMF); WATSON, 1897 (as *M. medicago* n.sp.): Madeira, Punta de Lourenço to 50 fms. (91 m); Magdalena (dredged); Selvagem Grande, shore; NOBRE, 1937 (as *M. medicago*): same as above, and Funchal; NORDSIECK & GARCIA-TALAVERA, 1979 (as *M. medicago*): Madeira.

Remarks: No live specimens but only fresh dead specimens have been recorded until now by us. The species is apparently rare in the Archipelago (as it generally is elsewhere). There are only a few synonyms, amongst them *Murex medicago* Watson, 1897, described from Madeira.

Subfamily ERGALATAXINAE
Genus *Cytharomorula* Kuroda, 1953

Cytharomorula grayi (Dall, 1889)
Figs 5-6

Nassarina grayi Dall, 1889: 183, pl. 32, fig. 12a.

Trophon lowei Watson, 1897: 244, pl. 19, fig. 12.
Trophon lowei -NOBRE, 1937: 28.
Urosalpinx lowei -NORDSIECK & GARCIA-TALAVERA, 1979: 134.

Records: Some live and dead taken specimens from Madeira (with no precise locality data, and Funchal Bay) and from Porto Santo, up to 100 m. depth (MMF); WATSON, 1897 (as *Trophon lowei* n.sp.): Madeira, 50 fms (91 m) (Labra and Punta de São Lourenço); NOBRE, 1937 (as *T. lowei*): same as above; NORDSIECK & GARCIA-TALAVERA (as *Urosalpinx lowei*): Madeira.

Remarks: *Nassarina grayi* was described from Barbados (West Atlantic), *Trophon lowei* from Madeira and a third synonym, *Cantharus laevis* Smith, 1891, was described from St. Helena. The species is also known from the Canary Islands. It is now classified in the Muricidae, subfamily Ergalataxinae, due to morphological affinities of shell and radular characters with other species of the subfamily. The geographical distribution is probably world-wide because closely related specimens, probably belonging to the same species, have been recorded from the Indian and Pacific Oceans.

Genus *Orania* Pallary, 1900

Orania fusulus (Brocchi, 1814)

Murex fusulus Brocchi, 1814: 409, pl.8, fig.9.

Records: NOBRE, 1937: Funchal; Porto Santo; NORDSIECK & GARCIA-TALAVERA, 1979: Madeira.

Remarks: The species is not yet recorded by us, but its presence in Madeira is not doubted due to its presence from the Mediterranean Sea to Angola (West Africa).

Subfamily OCENEBRINAE
Cossmann, 1903
Genus *Ocenebra* Gray, 1847

Ocenebra erinaceus (Linné, 1758)
Fig. 7

Murex erinaceus Linné, 1758: 748.

Murex (Ocinebra) erinaceus -WATSON, 1897: 294.
Murex erinaceus -NOBRE, 1937: 28.
Ocenebra erinaceum -NORDSIECK & GARCIA-TALAVERA, 1979: 132.

Records: Madeira (many localities); Porto Santo; Desertas Is, many live and dead taken specimens (MMF); WATSON, 1897: from Funchal to East point and Porto Santo (abundant); NOBRE, 1937: same remarks as above; NORDSIECK & GARCIA-TALAVERA, 1979: Porto Santo.

Remarks: The species is common in the Archipelago. It is also common in the Eastern Atlantic and the Mediterranean sea, with a lot of synonyms, because of the many shell variations.

Subgenus *Ocinebrina* Jousseaume, 1880

Ocenebra (Ocinebrina) edwardsi
(Payraudeau, 1826)
Figs 9-10

Purpura edwardsi Payraudeau, 1826: 155, pl. 7, fig. 19, 20.

Murex (Ocinebra) edwardsii -WATSON, 1897: 294.
Murex edwardsi -NOBRE, 1937: 28.
Ocinebrina edwardsi -NORDSIECK & GARCIA-TALAVERA: 133.

Records: Madeira (loc.inc.) (MMF); WATSON, 1897: from Funchal westwards. Very abundant; NOBRE, 1937: Funchal, Porto Santo; NORDSIECK & TALAVERA, 1979: Madeira.

Remarks: Numerous specimens are present in the collections of the Museum of Funchal, all from Madeira, but with no precise locality data. The species is widely dispersed in the Mediterranean and the East Atlantic Ocean, and many forms have been named. All specimens examined from Madeira are strongly spirally sculptured, with low, broad axial varices.

Ocenebra (Ocinebrina) aciculata (Lamarck, 1822) Fig. 8

Murex aciculatus Lamarck, 1822: 176

Murex (Ocinebra) aciculatus -WATSON, 1897: 294.
Murex aciculatus -NOBRE, 1937: 29.
Ocinebrina aciculata -NORDSIECK & GARCIA-TALAVERA, 1979: 133.

Records: Madeira (Ponta Gorda), Porto Santo and the Desertas Is (common) (MMF); WATSON, 1897: from Madalena to island's East point and Porto Santo; NOBRE, 1937: from Madalena to East point; Porto Santo; Funchal, Pontinha; Porto Santo; NORDSIECK & TALAVERA, 1979: Madeira.

Remarks: A small species, reaching a maximum length of 15 mm. It is common in the Eastern Atlantic and the Mediterranean Sea. It is not variable morphologically, however some form names have been proposed for smaller, larger, or more colourful specimens.

Ocenebra (Ocinebrina) inordinata n.sp. Figs 11-13

Type material: Madeira Is (no other locality data), **holotype** MMF 25429, 19.2 mm; 1 paratype coll. R. Houart, 14.2 mm; 1 paratype coll. J. Verstraeten, 21 mm.

Description: Shell medium sized for the subgenus, up to 21 mm in length at maturity, heavy, tuberculate. Spire high with 1.25-1.50 protoconch whorls and up to 6 shouldered, strongly nodose teleoconch whorls. Suture appressed. Protoconch whorls rounded, weakly elongate, smooth; terminal varix very shallow, nearly straight.

Axial sculpture consisting of ridges and varices: 12 low axial ridges on first teleoconch whorl; 11 on second whorl; 10 or 11 low to high ridges on third whorl; 9 high, strong ridges on 4th whorl; 7 high ridges, and varices on 5th whorl; last teleoconch whorl with 4 or 5 erratically placed varices, some with low, blunt open spines, and one or two high, strong axial node.

Spiral sculpture consisting of 2 nodose cords on first teleoconch whorl; 2 primary cords and 1 secondary cord on the shoulder on second whorl; third to fifth teleoconch whorls with 2 primary cords and narrow threads between them, some 2 or 3 additional threads on shoulder; last teleoconch whorl with 5 or 6 low, obsolete cords, forming short, rounded, broadly open spines on the varices, chiefly on apertural varix. Occasionally with 2 or 3 low, shallow threads between cords.

Aperture ovate, moderately large. Columellar lip smooth, margin partially weakly erect, adherent at adapical extremity. Anal notch broad. Outer lip erect, smooth, with 5 or 6 strong nodes within, adapical node strongest.

Siphonal canal short, narrow, straight, closed, smooth.

Shell entirely light brown; aperture glossy white.

Remarks: We are aware of the great diversity of forms existing in the *Ocenebra (Ocinebrina) edwardsi* group of shells, but *O. inordinata* does not fit any of these forms. A great number (more than 500 specimens) of *O. edwardsi* were observed from different localities, representing many varieties (both colour and morphological forms). Moreover, the varieties of *O. edwardsi* are generally mixed, and many forms live together in the same region. We also examined more than 200 specimens of *O. edwardsi* from Madeira, all are very similar morphologically.

Ocenebra inordinata constantly differs in its completely white aperture, in the few, strong nodes on its last whorl, and in the erratically placed varices with blunt, broad, open spines. One form of *O. edwardsi* (valid taxon?) from Vigo (Spain) has a completely white aperture, with a white shell, but it differs strongly morphologically from *O. inordinata*. That shell was illustrated by ROLAN (1983: 231) as *Ocinebrina* cf. *nicolai* (Monterosato, 1884).

From *O. miscowichi* (Pallary, 1920), a species occuring off the North-West African coast, *O. inordinata* differs in its white aperture, stronger and higher axial sculpture, in its erratically placed varices, and in its fewer, broader spiral cords.

Other species of European or West African Ocenebra or Ocinebrina are very different and need not to be compared.

Etymology: *inordinata* (Latin): not arranged, disorderly. Named for the erratically placed varices and axial ridges.

Genus *Bedeva* Iredale, 1924

Bedeva paivae (Crosse, 1864)
Figs 15-17

Trophon paivae Crosse, 1864: 278.

Records: Madeira, Funchal Harbour, 0-10 m, many specimens.

Remarks: *Bedeva paivae* was originally restricted to Australia, from South Queensland to Shark Bay, West Australia, and in Tasmania (WELLS & BRYCE, 1986). KILBURN & RIPPEY (1982: 91) recorded the species from the eastern Cape Province (South Africa) where it lives in colonies of up to 72 individuals per square meter. *Bedeva paivae* was also collected alive in the Canary Islands (GOMEZ, 1983). It is obvious that the species was introduced to South Africa, to the Canary Islands, and now to the Archipelago of Madeira in the hull of ships (oil tankers, merchant ships...), as already noted in KILBURN & RIPPEY (1982) and in GOMEZ (1983). The presence of *B. paivae* in the Archipelago of Madeira was never reported before. It is apparently very common but not outside of the harbour. The first known specimen was collected by Nicolas Vassart.

The classification of *Bedeva* in the Ocenebrinae is tentative and based on the observation of radular morphology (Vokes, pers. comm.).

Subfamily TROPHONINAE
Genus *Trophonopsis* Bucquoy & Dautzenberg, 1882

Trophonopsis richardi
(Dautzenberg & Fischer, 1896)

Trophon richardi Dautzenberg & Fischer, 1896: 438, pl. 18, fig. 6.

Records: NORDSIECK & GARCIA-TALAVERA, 1979: Madeira.

Remarks: No recent record is known for this species. Moreover, the real identity of the recorded species in NORDSIECK & GARCIA-TALAVERA (1979: 132) is very doubtful because of the confusion existing between *Trophonopsis muricatus* (Montagu, 1803) and *Trophonopsis richardi* (Dautzenberg & Fischer, 1896) (= *Trophon droueti* Dautzenberg, 1889) (HOUART, 1981: 33). The presence of *T. droueti* or *T. muricatus* in the Archipelago thus remains doubtful.

Subfamily TYPHINAE
Genus *Typhis* Montfort, 1810
Subgenus *Typhinellus* Jousseaume, 1880

Typhis (Typhinellus) fistulatus
(Risso, 1826)

Murex fistulatus Risso, 1826: 191 (not *Muricites fistulatus* Schlotheim, 1820 = *Lyrotyphis*).

Typhis sowerbii Broderip in Broderip & Sowerby 1833: 178.

Records: NORDSIECK & GARCIA-TALAVERA, 1979: Madeira (as *Typhis sowerbyi* Broderip, 1833).

Remarks: The record of this species in Madeira is probably based on a misidentification. The specimen in the possession of Garcia-Talavera (from the Canary Islands) is an example of *Typhis (Typhina) belcheri* Broderip, 1833. Moreover, Garcia-Talavera (pers. comm.) has no material from Madeira. The presence of *Typhis fistulatus* in the Archipelago of Madeira is rejected here.

Subfamily RAPANINAE (ex Thaidinae)
Genus *Stramonita* Schumacher, 1817

Stramonita haemastoma (Linné, 1767)
Fig. 14

Buccinum haemastoma Linné, 1767: 1202.

Purpura haemastoma -WATSON, 1897: 306.
Purpura haemastoma -NOBRE, 1937: 30.
Thais haemastoma -NORDSIECK & GARCIA-TALAVERA, 1979: 132.

Records: Many live and dead taken specimens from the Desertas Is and the Selvagens Is (MMF); WATSON, 1897: Everywhere, very common; NOBRE, 1937: Porto da Cruz, Funchal, Porto Santo, Zimbral; NORDSIECK & GARCIA-TALAVERA, 1979: Madeira.

Remarks: *Stramonita haemastoma* is variable and is recorded from both the eastern and western Atlantic. It also occurs all along the West African coast, as well as in the Mediterranean Sea. Many synonymous names and a few subspecies have been proposed for this species.

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Figures 1-8 (opposite page).

1-2. *Hexaplex trunculus* (Linné, 1758), Madeira, Garajau, 70, MMF.
  1. 83.3 mm.
  2. 41.2 mm.

3-4. *Muricopsis (Murexsul) aradasii* (Monterosato, 1883).
  3. *Murex medicago* Watson, 1897. Holotype BMNH 1911.7.17.3, 13.5 mm.
  4. Madeira, Caniçal, MMF JSL-3004, 13 mm.

5-6. *Cytharomorula grayi* (Dall, 1889).
  5. *Trophon lowei* Watson, 1897. Holotype BMNH 1911.7.17.2, 19 mm.
  6. Madeira (no other locality data), MMF, 19.5 mm.

7. *Ocenebra erinaceus* (Linné, 1758), Madeira (no other locality data), MMF 24702, 44.1 mm.

8. *Ocenebra (Ocinebrina) aciculata* (Lamarck, 1822), Madeira Arch., Desertas, MMF 25160, 10.8 mm.


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Figures 9-14 (opposite page).

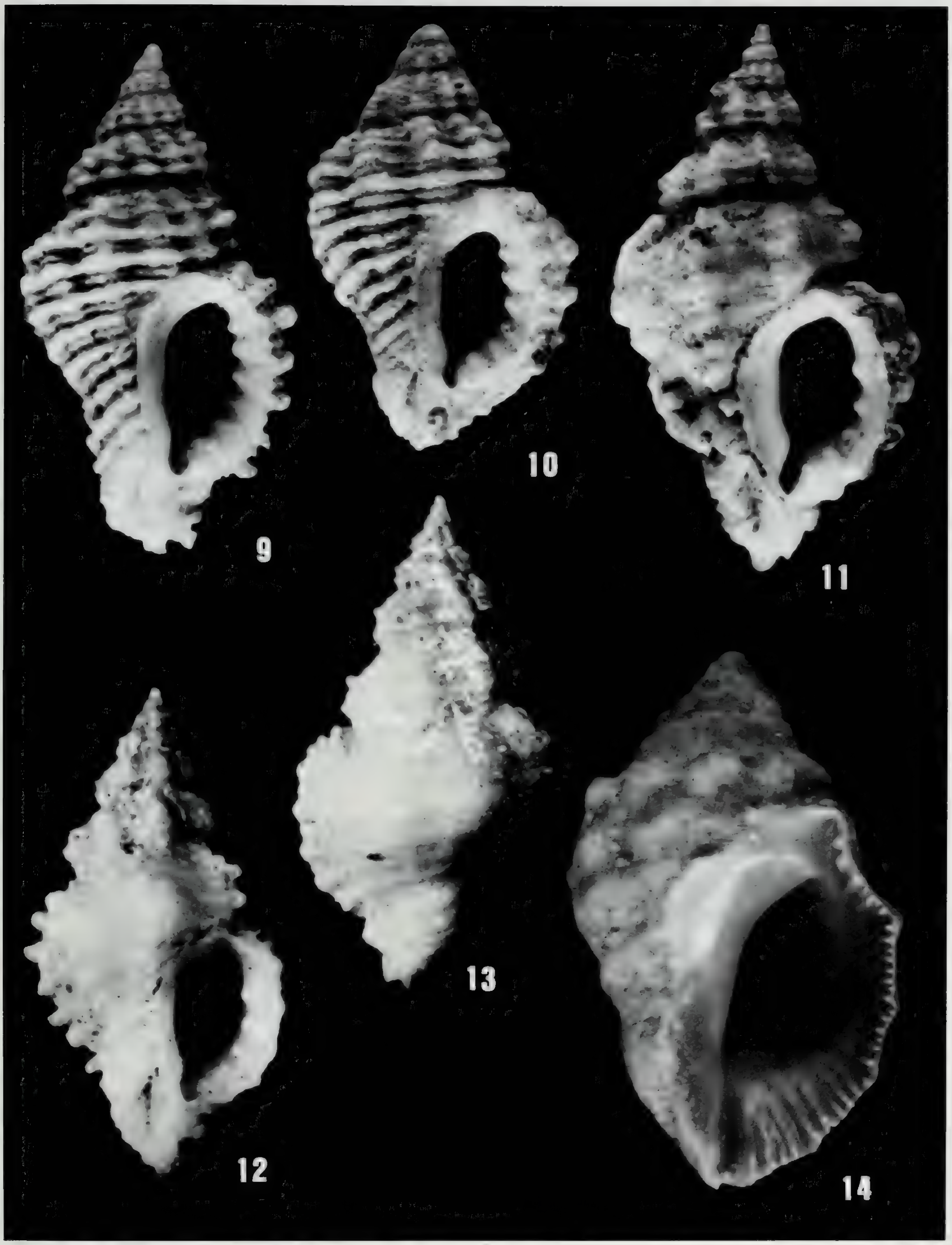
9-10. *Ocenebra (Ocinebrina) edwardsi* (Payraudeau, 1826), Madeira (No other locality data), MMF 24631. 9: 17 mm. 10: 14 mm.

11-13. *Ocenebra (Ocinebrina) inordinata* n.sp.

11. Holotype MMF 25429, 19.2 mm.

12-13. Paratype coll. J. Verstraeten, 21 mm.

14. *Stramonita haemastoma* (Linné, 1767), Madeira Arch., Selvagens, MMF 14332, 60.3 mm.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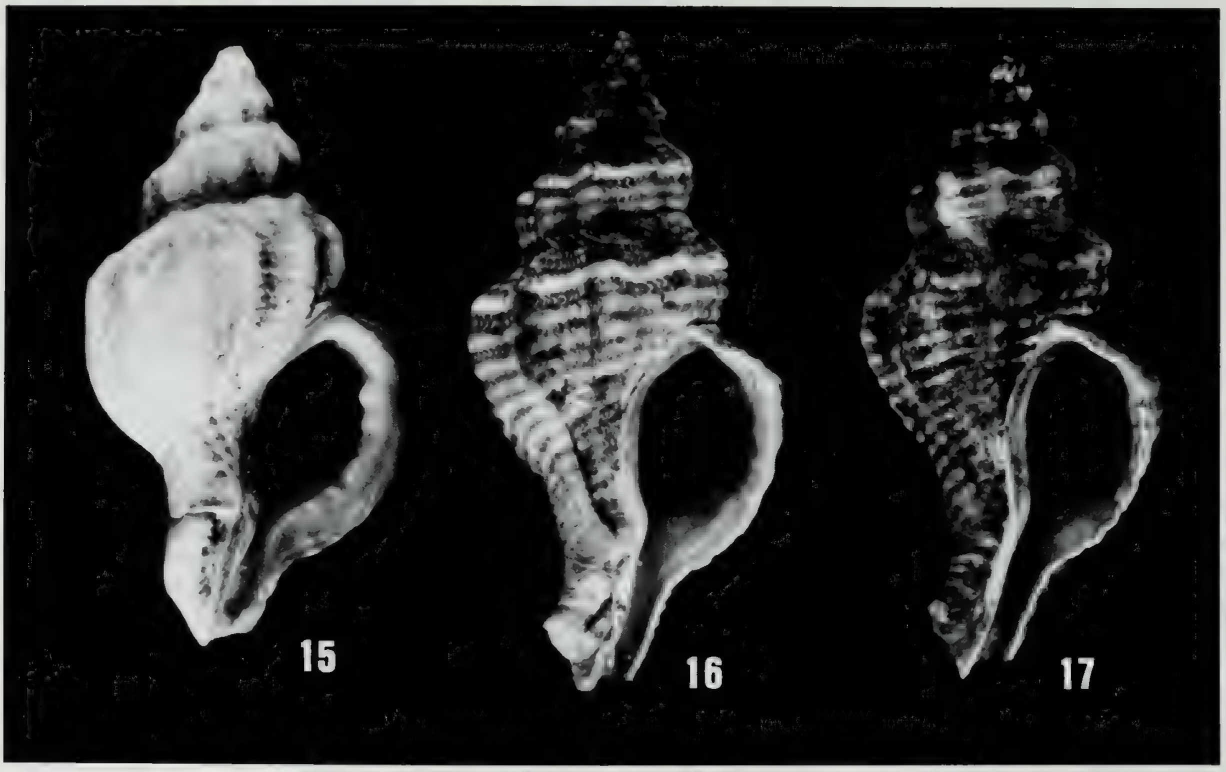

Figures 15-17.

15-17. *Bedeva paivae* (Crosse, 1864).
15. Syntype BMNH 1870.10.26.70, 24 mm.
16-17. Funchal Harbour, Funchal, Madeira Arch., RH, 16: 19.2 mm; 17: 16.8 mm.

The scale of sympatry in the genus *Oliva* (Gastropoda, Olividae) (°)

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KEYWORDS. Sympatry, syntopy, variation, taxonomy, Mollusca, Gastropoda, *Oliva*.

ABSTRACT. Sharp morphological discontinuities have been evidenced between conspecific, close neighbouring *Oliva* populations in Hansa Bay (Papua New Guinea). Taxonomic implications are discussed. The broad notion of sympatry usually applied in the genus *Oliva* should be replaced by that of syntopy.

RESUME. De nettes discontinuités morphologiques ont été mises en évidence entre des populations conspécifiques très voisines d'*Oliva* à Hansa Bay (Papouasie- Nouvelle-Guinée). Les implications taxonomiques sont discutées. La notion large de sympatrie habituellement appliquée au genre *Oliva* devrait être remplacée par celle de syntopie.

1. INTRODUCTION

Much more effort has been invested on the nomenclature of *Oliva* species than on their natural history. The taxonomy of this genus (like that of the immense majority of marine molluscs) is therefore still at the stage of the morphospecies approach, based upon the demonstration of gaps in the distribution of shell characters. This method is obviously open to errors. Some are inherent to the method itself (amongst others, it is likely to overlook sibling species). Other errors can result from the quality of data (these vary from the statement of personal impressions to multivariate analysis, depending on the requirements of authors). I wish to report and discuss here some data which underline another, frequently overlooked, possible source of error: unwarranted assumptions on sympatry.

Data on sympatry are indeed crucial because they largely determine the reasoning of the morphospecies taxonomist. On the one hand, if two sympatric populations are separated by a constant morphological gap, one can infer that interbreeding does not take place and that one deals with two distinct species. In the absence of potentially misleading factors (such as sexual dimorphism, for instance) this procedure is quite straightforward. On the other hand, one can reasonably combine allopatric, morphologically distinct populations into one species if one establishes that their discriminating characters are bridged by other populations, forming one *morphological continuum*. In this case, one cannot exclude potential interbreeding. Decisions on allopatric populations are of course more delicate (see MAYR & ASHLOCK, 1991) and their reliability will depend very much on the quality of the data.

Suspicion of sympatry-related errors arose during a study on the "*Oliva oliva* complex" (TURSCH *et al.*, 1992). The existence of separate species was detected at the local level by the observation of total morphological gaps between sympatric populations. On a global scale, the populations of each species form a morphological continuum. As one could expect, extreme forms of the same species (sometimes separated by hundreds or thousands of miles) often differ to the point of complete morphological separation. But these differences were always bridged in intermediate, allopatric populations. In contrast, each conspecific continuum is separated from the others by demonstrable gaps reflecting the boundaries of intraspecific variability.

Although the overall picture was quite satisfactory, unexpected facts were observed in two localities (MISSA, 1991; TURSCH *et al.*, 1992). In Phuket (Thailand) one finds two morphs that are locally entirely separable, while being obviously bridged by series of allopatric intergrades. An entirely similar situation occurs in Carita Beach (Java). These observations were rather disquieting, all the more so because similar situations were soon detected in several other

(°) This is paper 21 in the series *Studies on Olividae* and Laing Island Biological Station contribution n° 286.

Oliva species, as will be seen here below. On the one hand, membership of the same morphological continuum is a very strong argument for conspecificity. On the other hand, sympatric forms separated by an absolute morphological gap just have to be distinct species, at least in groups such as *Oliva* where sexual dimorphism and allometry are absent or negligible.

This apparent contradiction could be explained by invoking circular overlap, a situation in which the extremities of a chain of interbreeding local races come into contact and where the extreme forms, now sympatric, cannot anymore interbreed. A much simpler explanation would be that there is something wrong in the way we usually apply the concept of sympatry to *Oliva* (and possibly many other marine molluscs).

Sympatry has been conceived broadly to include "*populations the individuals of which are within cruising range of each other during the breeding season, even though the habitats in which they occur do not overlap in space*" (CAIN, 1953; MAYR, 1963; MAYR & ASHLOCK, 1991). We know very little on cruising ranges, yet the common practice of marine mollusc taxonomy is to consider as sympatric two populations separated by a few miles, living in the same depth range and on the same type of sediment.

The hypothesis of a possible error in our application of the concept of sympatry to the genus *Oliva* could be tested by studying intraspecific variation over very short distances. A suitable location for such a study was provided by Hansa Bay, on the North coast of Papua New Guinea. It is a small semicircular bay (roughly 10 km in diameter) located in Madang Province, near the mouth of the Ramu River, about 110 nautical miles West of Madang. A rough sketch of Hansa Bay is given in Fig. 1. Laing Island (4°10'30"S-144°52'20"E) lying roughly at the middle of the bay is a raised coral reef, covered with vegetation and separated from the mainland by depths of 45-50 m, with a muddy bottom. Climatic and hydrological data are given by BOUILLON *et al.* (1986). Detailed environmental data can be found in CLAEREBOUDT (1989). The sediments in which *Oliva* are found in Hansa Bay have been analysed by VAN OSSELAER (1992) (see VAN OSSELAER *et al.*,1994). All the coast is lined with a long, black sand beach, with the exception of a small stretch at Boro Beach, formed of white, coarse coral sand.

The *Oliva* species of Hansa Bay have been under survey for nearly 20 years, since the establishment of King Leopold III Biological Station on Laing Island in 1974. 29 species have been found so far and nearly all of them have been collected in adequate numbers, with accurate locality data. Many of these species have distinct micropopulations, separated by short distances. The differences observed between these populations concern not only the variations of colour pattern observed in cryptic, polytopic species (VAN OSSELAER *et al.*, 1994) but also, as will be shown here, the morphology of the shell. In order to avoid repetition, only three cases (ranging from a rather subtle discontinuity to a large, obvious morphological gap) will be described here, although many additional examples could be given.

2. MATERIAL AND METHODS

2.1. Collection

Oliva specimens have been obtained mostly by SCUBA diving (day and night dives) but a variety of other methods have also been used. These include dredging (using a small rectangular steel mesh dredge with an opening of 60 x 22 cm), trawling (with a small mesh 3 m rigid frame trawl), snorkelling in shallow waters, or beach collecting at the turn of the low tide. Baiting and trapping have often been used. Quantitative quadrats and transects have also been effected (VAN OSSELAER, 1992). When diving, small rigid steel mesh "hand dredges" (in the shape of a dustpan, about 20 x 30 cm) have been especially productive. Special care has always been taken to avoid overcollecting. Specimens of all 29 *Oliva* species present in Hansa Bay have been kept and observed in aquaria, sometimes for several months.

2.2. Nomenclature

Oliva amethystina (Röding, 1798) was formerly part of *O. annulata* (Gmelin, 1791), a *nomen dubium* encompassing at least two distinct species (TURSCH *et al.*, 1986). The nomenclatural puzzle of the "*O. oliva* complex" is not yet completely solved (see TURSCH *et al.*, 1992), so for the time being, the name *O. smithi* Bridgmann, 1906 will be used for one of the species discussed here. This name is probably a junior synonym but has been selected because it is based upon indisputable type material.

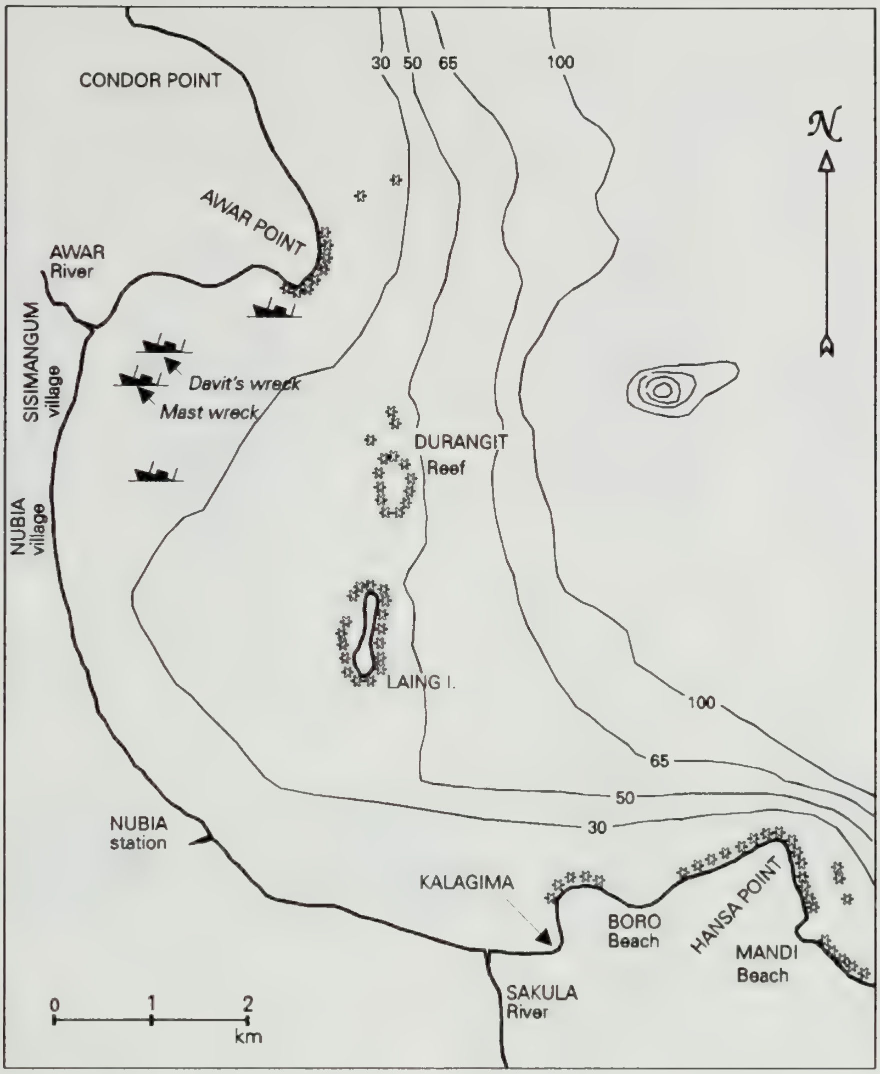

Fig. 1. Hansa Bay.

2.3. Material measured

BT-numbers refer to specimens in the author's collection, DG- numbers to the collection of Dr. Dietmar Greifeneder (Schwenningen) and JS- numbers to that of Dr. Jacques Senders (Brussels).

Oliva amethystina (Röding, 1798).

PAPUA NEW GUINEA, HANSA BAY: - DURANGIT REEF, 6m: specimens BT-7002, BT-7003, BT-7004, BT-7006 to BT-7001; - "DAVIT'S WRECK" (near Awar river), 6 m: specimens BT-6779 to BT-6786; - "MAST WRECK" (near Awar river), 5 m: specimens BT-7178 to BT-7182.

OTHER LOCALITIES: SOLOMON IS. : specimens BT-2454, BT-3512, BT-3516, DG-2521/5, DG-2521/8, DG-2523/6, DG-2524/3.

Oliva smithi Bridgmann, 1906.

PAPUA NEW GUINEA, HANSA BAY: - LAING ISLAND West coast (lagoon), 0.5-1 m: specimens BT-2174 to BT-2183. - OFF BORO BEACH, 6-8 m: specimens BT-2164 to BT-2173.

OTHER LOCALITIES: AUSTRALIA (North Queensland): specimens BT-5767, BT-5807, BT-5808, BT-6122 to BT-6126, BT-6128, BT-6130; INDONESIA (Ceram I.): specimens BT-167, BT-169, BT-296, BT-298; PHILIPPINES (Cebu): specimens BT-1312, BT-4999 to BT-5003, BT-5789, BT-5791 to BT-5793; PHILIPPINES (Pamilacan): specimens BT-6277 to BT-6279, BT-6281, BT-6284.

Oliva oliva (Linnaeus, 1758).

PAPUA NEW GUINEA, HANSA BAY: - BORO BEACH, low tide: specimens BT-2154 to BT-2163 (all of very light ground colour, hereunder designated as "white"). - SISIMANGUM BEACH, low tide: specimens BT-2154 to 2158 (all of very light ground colour, hereunder designated as "white") and specimens BT-2149 to BT-2153 (all of very dark ground colour, hereunder designated as "black").

OTHER LOCALITIES: PAPUA NEW GUINEA (Samarai, Milne Bay): specimens BT-5245 to BT-5247, BT-5251, BT-5254, BT-5259, BT-5263, BT-5269, BT-5272, BT-5273; PHILIPPINES (Zamboanga): specimens BT-4589 to BT-4593, BT-5700, BT-5779 to BT-5784; THAILAND (Patong Beach, Phuket): specimens BT-4768, BT-6142, BT-6149, BT-6154, JS-035, JS-037, JS-040, JS-176, JS-186.

In addition to the measured material, several hundred Hansa Bay specimens of the most common populations of these species have been visually checked, in order to verify the constancy of the discriminating characters described below.

2.4. Tests of conspecificity.

Special care was taken to verify that the populations presented here as conspecific do really belong to the same species. All are common, widely distributed *Oliva* species for which abundant comparison material is available. In each case it was established (by principal factor analysis and/or discriminant factor analysis) that these populations are parts of a much larger morphological continuum, covering the whole distribution area of the species. Within a species continuum, no population (or group of populations) could be distinguished from all the others by any of the many metric shell variables that were tested (alone or in combination). Examples of the applications of these methods to *Oliva* have already been reported (for instance in TURSCH *et al.*, 1992) and, for the sake of brevity, details of these lengthy procedures will not be reported here. For every case, it was demonstrated (by scatter diagrams) that the morphological gaps distinguishing the Hansa Bay populations are bridged in other, allopatric populations. For each species, only one scatter diagram will be illustrated here. One should note that the "bridging populations" do not necessarily occur in Hansa Bay.

2.5. Measurements

The following measurements have been used in this paper: H, L, D (Fig. 2) and R (Fig. 3) are teleoconch measurements defined in TURSCH & GERMAIN (1985). Pat15, pat16, pat17 and pat18 (Fig. 4) are protoconch measurements defined in TURSCH & GERMAIN (1987).

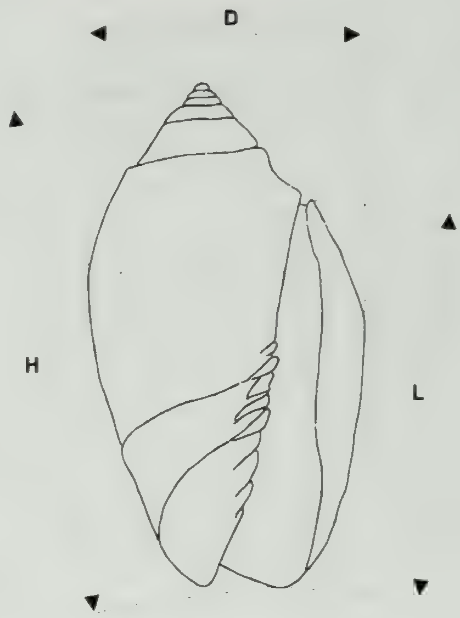

Fig. 2. Sketch of the measurements H, D and L.

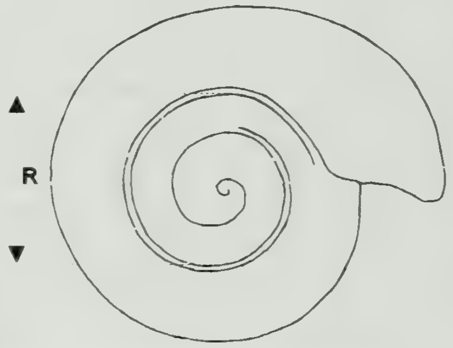

Fig. 3. Sketch of the measurement R.

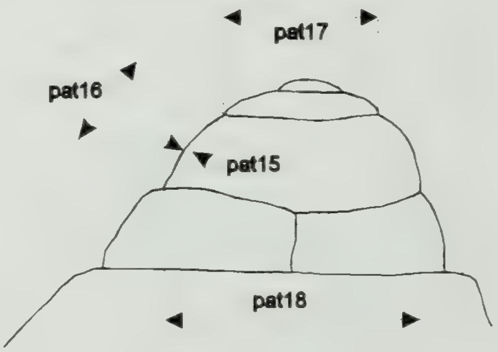

Fig. 4. Sketch of the protoconch measurements pat15, pat16, pat17 and pat18.

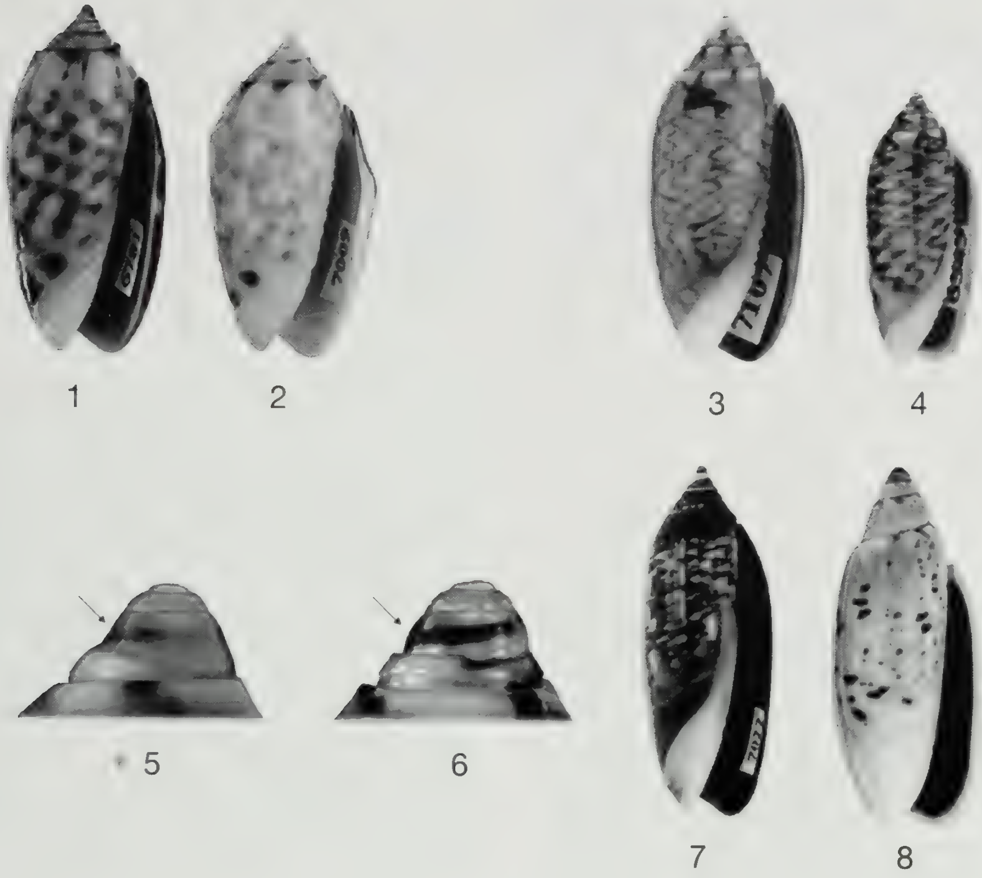

Plate 1.

Figs. 1-2: *Oliva amethystina* (Röding, 1798).

Fig. 1. Typical specimen (BT-6781) from "Davit's wreck", 6 m.

Fig. 2. Typical specimen (BT-7009) from Durangit Reef, 6 m.

Figs. 3-4: *Oliva smithi* Bridgman, 1906.

Fig. 3. Typical specimen (BT-7107) from Laing I. lagoon, 0.5-1 m.

Fig. 4. Typical specimen (BT-6543) from Boro Beach, 6-8 m.

Figs. 5-6: Protoconchs of *Oliva smithi*. Note the difference in convexity of the penultimate protoconch whorl (arrows) and the fusion of the two last protoconch whorls in specimen BT-7107 (fig. 5).

Fig. 5. Protoconch of specimen BT-6225 from Laing I. lagoon, 0.5-1 m.

Fig. 6. Protoconch of specimen BT-6543 from Boro Beach, 6-8 m.

Figs. 7-8: *Oliva oliva* (Linnaeus, 1758).

Fig. 7. Typical specimen (BT-7022) from Sisimangum Beach, low tide.

Fig. 8. Typical specimen (BT-6573) from Boro Beach, low tide.

3. OBSERVATIONS AND RESULTS

3.1. *Oliva amethystina* (Röding, 1798).

In Hansa Bay, this common species lives mostly between -1 and -10 m, exclusively in coral sand, in proximity to live coral (where it is easily mistaken for a dead *Acropora* coral fragment). Two populations (Plate 1, figs. 1-2) have been compared: one living on the top of Durangit Reef and another living around "Davit's wreck", two localities distant of only 2.8 km and separated by a bottom of very fine dark mud, in 40-48 m, extending over about 1 kmMany specimens have been collected at -6 m, in coarse, white coral sand, on the top of the large Durangit Reef. This biotope is often exposed to heavy water motion (high waves and swift current), so *Oliva* tracks are immediately erased and specimens have to be collected with a small hand dredge. Adult specimens are mostly found around the rocky ledges of the sand pockets, while juveniles are mostly found in the sand ripples. The population of *O. amethystina* at the top of Durangit Reef is very similar to (and could not be separated from) that of the Laing Island reef (excepted that the percentage of large, adult shells is much higher at Durangit).

A much smaller number of specimens were collected at -6 m, around a Japanese wreck called "Davit's wreck" because its davits could be seen above water until a few years ago. The specimens lived in a mixture of fine and coarse coral sand(including dark terrigeneous material). In this biotope where the water is mostly quiet, all our juvenile *amethystina* were found (by hand dredging) only in the white coral sand recently deposited just along the hull, whereas some adults were found by their tracks in the darker sand further away from the wreck. The wreck is quite small and we have been careful not to overcollect this little biotope. The shells are quite characteristic and no matching specimens have been found in or around Hansa Bay despite extensive exploration over 20 years, with the exception of a few rather similar specimens found around "Mast wreck", another sunken ship lying close to "Davit's wreck". The two wrecks are separated by about 200 m of hard, fine dark sediment, in 5-7 m depth.

All available specimens (8) from "Davit's wreck" were compared to an equivalent number of randomly selected specimens from Durangit. The two samples differ by protoconch as well as by teleoconch characters and are completely separable, as demonstrated (Fig. 5) by a scatter diagram of pat17/pat18 *vs*. D/L (pat17/pat18

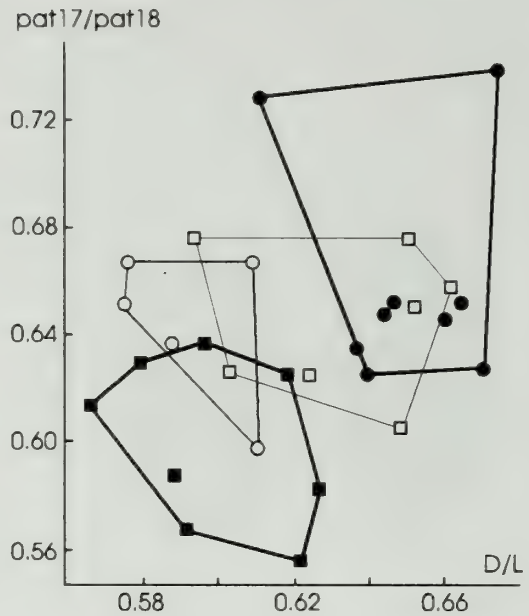

Fig. 5. Comparison of populations of *Oliva amethystina*. Scatter diagram of D/L *vs*. pat17/pat18. Minimum convex polygons. The populations from Hansa Bay (thick contour lines - black circles: shells from Durangit Reef - black squares: shells from "Davit's wreck") are separated by an obvious moprphological gap. This gap is bridged by other conspecific populations (thin contour lines - white circles: shells from "Mast wreck" - white squares: shells from Solomon Is.).

roughly reflects the conical angle of the penultimate protoconch whorl). All specimens collected at Durangit are squat, heavy, with a tendency to bulge on the body whorl (Plate 1, fig. 2); all have a light coloured background. All specimens from "Davit's wreck" are more slender, have a darker background (Plate 1, fig. 1) and the surface of their protoconch is mostly corroded. This is also the case for the "Mast wreck" specimens. Fig.5 also shows that the morphological gap separating the Durangit Reef and the "Davit's wreck" populations is bridged in other, allopatric populations of the same species.

It should be noted that "Davit's wreck" was sunk during World War II. Like the other wrecks in the bay, it is now overgrown with a luxuriant reef, the decay of which surrounds the hull with coral sand, the exclusive habitat of *O. amethystina*. This small pocket of white coral sand is isolated in a plain of fine black sediment. If one estimates the time required for the

growth and the subsequent decay of the coral it is unlikely that the "Davit's wreck" population of *O. amethystina* is more than 30 years old.

3.2. *Oliva smithi* Bridgman, 1906.

Two distinct populations of this common species are found in Hansa Bay (Plate 1, figs. 3-4). One is widely spread along the coast, in depths of 2-14 m (generally 5-9 m), on sediments ranging from fine, dark terrigeneous material (off Awar, in usually quiet waters) to fine, white coral sand (off Boro Beach, where the sediment is in nearly constant motion, due to heavy swell). The colour pattern of the shells is very variable, mostly matching the colour of the sediment.

The other population has a very restricted distribution in the lagoon of Laing Island, in shallow water (0.5-1 m), coarse coral sand, occasional moderate wave action, and is quite constant in colour pattern. It is a recent (maybe accidental) introduction, not found before 1992 although the lagoon has been the object of regular, intensive search for 20 years. Furthermore, the lagoon population happens to live in the place where our native co-workers (all experienced *Oliva* watchers) daily wash their dishes, and it is unlikely that the shells would have escaped their trained eye for very long. The lagoon beach appears quite uniform, but during a thorough search in early 1993, *O. smithi* was found only on a stretch of about 50 meters. Only a few shells were gathered, in order not to upset this small population.

A sample of *O. smithi* from Laing Island lagoon was compared to a sample from off Boro Beach. These localities are roughly 3.8 km apart and are separated by a bottom of very fine dark mud, at 40-48 m, extending over about 1.5 km. The two samples are completely separated (Fig. 6) on a scatter diagram of D/L *vs.* pat15/pat16 (pat15/pat16 is an expression of the convexity of the penultimate nuclear whorl). Specimens from Laing Island reach a larger size than the Boro Beach shells (H_{max} 22.8 mm *vs.* 15.8 mm) and their body whorl is less cylindrical (see Plate 1, figs. 3-4). The protoconchs of the two samples, albeit similar, show constant differences (see Plate 1, figs. 5-6). In the Laing Island specimens, the two last whorls of the protoconch are fused (the suture is covered by a thin, transparent layer of enamel) and the profile of the penultimate nuclear whorl is quite flat. In the Boro Beach specimens, the two last whorls of the protoconch are distinct and the profile of the penultimate nuclear whorl is convex. Fig.6 also shows that the morphological gap separating the Laing Island and the Boro populations is bridged in other, allopatric populations of the same species.

3.3. *Oliva oliva* (Linnaeus, 1758).

In Hansa Bay, this abundant species is restricted to the low water level on sandy beaches exposed to frequent surf. It is polytopic and cryptic (VAN OSSELAER *et al.*, 1994), the background colour of the shells ranging from very pale to very dark (hereafter called "white" and "black" shells).

One small population lives on white, coarse coral sand at Boro Beach, where heavy swell is generally prevalent. Specimens from Boro (see Plate 1, fig. 8) reach a moderate size (H_{max} 33.15 mm). All 42 specimens collected are "white" and have an elongated spire. The aperture is short and consistently reddish brown. The protoconch of all specimens is severely eroded.

Another population (this one very large) extends all the way from the northern tip of the bay to the mouth of the Sakula river, on fine, black volcanic sand, with occasional, moderate swell. Specimens from Sisimangum (see Plate 1, fig. 7) reach a larger size (H_{max} 42.31 mm). On nearly one thousand specimens observed, 76% are "black", 15 % are "white" and 9 % do not fit into these categories. The spire is short, the aperture long and mostly dark purple. Most specimens have an intact protoconch.

A sample of 10 specimens (all "white") from Boro Beach was compared to a sample of 10 specimens (5 "white", 5 "black", all protoconchs intact) from Sisimangum. These localities are distant of roughly 12 km along the coast but the Sisimangum population reaches the Sakula river and the two populations actually come within 1.5 km of each other. The only physical obstacles separating these populations are a small rocky point between Boro and Kalagima and the mouth of the Sakula River. The two samples are entirely distinct, separated by a large morphological gap, as shown (Fig. 7) on a scatter diagram of H/L *vs.* R/D. Within the Sisimangum sample, "white" and "black" specimens are not separated; shell morphology seems unrelated to colour. Fig. 7 also shows that the morphological gap separating the Sisimangum Beach and the Boro Beach populations is bridged in other, allopatric populations of the same species.

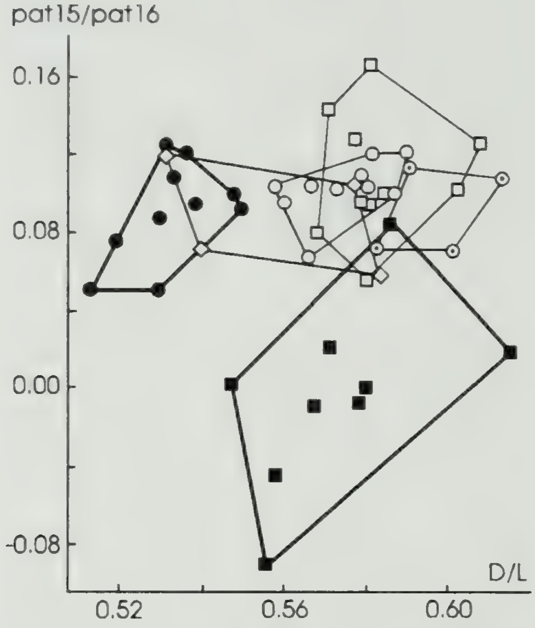

Fig. 6. Comparison of populations of *Oliva smithi*. Scatter diagram of D/L *vs.* pat15/pat16. Minimum convex polygons.

The populations from Hansa Bay (thick contour lines - black circles: shells from Boro - black squares: shells from Laing Island lagoon) are separated by an obvious moprphological gap. This gap is bridged by other conspecific populations (thin contour lines - white circles: shells from Australia, North Queensland - white squares: shells from Philippines, Cebu - white circles, centered: shells from Indonesia, Ceram - white lozenges: shells from Philippines, Pamilacan).

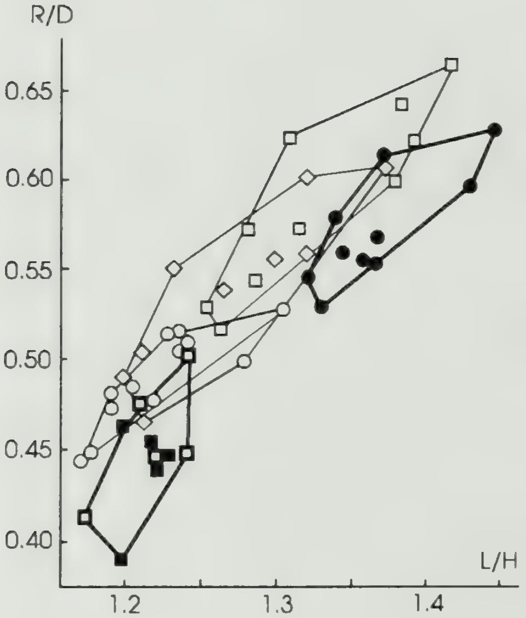

Fig. 7. Comparison of populations of *Oliva oliva*. Scatter diagram of D/L *vs.* pat15/pat16. Minimum convex polygons.

The populations from Hansa Bay (thick contour lines - black circles: shells from Boro Beach - black squares: black shells from Sisimangum Beach - thick white squares: white shells from Sisimangum Beach) are separated by an obvious moprphological gap. This gap is bridged by other conspecific populations (thin contour lines - white circles: shells from Philippines, Zamboanga - white squares: shells from Papua New Guinea, Samarai - white lozenges: shells from Thailand, Phuket).

It should be noted that the characters of these two populations have been stable for 20 years (judging from specimens in our collection) and probably for much longer a time, judging from specimens in ancient leg ornaments, still used in traditional *sing-sing* ceremonies by the local Dawar people.

4. INTERPRETATION

In short, it has been shown that:

a. Close neighbouring populations of the same *Oliva* species often present notable differences. These differences reach complete morphological separation in the examples presented here, but it should be stressed that this point is not essential. Some overlap in the distribution of population characters would not affect the conclusions here under. Many *Oliva* variants exhibit a remarkable fidelity to their locality, to the point that an experienced collector can often guess the precise origin of a given specimen.

b. The observed divergence of micropopulation characters can occur fast. It can be estimated to less than 30 years for *O. amethystina* (see section 3.1, last §) and to probably a few years for *O. smithi* (see section 3.2, § 2). In contrast, all the established populations regularly sampled for a long time have been stable in their characters at least over a period of 20 years and probably for much longer (see section 3.3, last §).

The observed differences in shell morphology could stem both from phenotypic plasticity and genetic isolation. On the one hand, environmental effects are probably an important contributor to colour variation, as illustrated by the fact that 24 of the 29 *Oliva* species encountered in Hansa Bay are cryptic to some degree, a phenomenon suggesting intense pressure from visual predator(s) (this is discussed in VAN OSSELAER *et al.*, 1994). Considerable predation has indeed been demonstrated in the case of *O. oliva,* where nearly every specimen of the Sisimangum population bears the scars of at least one unsuccessful attack (*study in progress*). No data for linking *Oliva* shell morphology to environmental effects are yet available.

On the other hand, genetic isolation is strongly suggested by the frequent observation of differences in the protoconch (*e.g.* in the case of *O. smithi*). The protoconch of *Oliva* species is produced inside the egg capsule (OLSSON & CROVO, 1968; TURSCH, 1991), where it is shielded against direct environmental influences. Morphological gaps at the protoconch level are thus likely to be of genetic origin. Another, indirect argument stems from the very rapid changes observed for the small population of *O. smithi* in the lagoon of Laing Island. Such a situation immediately evokes genetic drift, a phenomenon requiring genetic isolation.

One more indirect argument can be found in the morphological stability observed in established *Oliva* populations. This stability sharply contrasts with the rapid changes occurring in the topography of the shallow water biotopes of Hansa Bay. During the last 20 years, the beach at Sisimangum has diminished by some 100 m, the East coast and the northern tip of Laing Island have also considerably regressed, while the beach in the southern part of the lagoon has extended. According to the oral tradition of the local Dawar tribesmen, Laing Island was actually linked to the mainland at the time of their ancestors. Elderly people all say that in their youth Laing island had at least the double of its present size. In addition, sporadic eruptions of the nearby Manam volcano frequently pepper the whole area with large quantities of igneous material. The modifications of the shoreline produce important changes in physical conditions (slope, exposure to waves, etc.), to the point that some of our boat moorings had to be moved over the years. So the morphological stability of most populations shows that many of the discriminant characters used by the *Oliva* taxonomist do not reflect subtle environmental differences but most probably partial genetic isolation.

All the available data thus indicate that there appears to be severe restrictions on gene flow between many of the Hansa Bay conspecific *Oliva* populations. Each of these populations could be considered as a *topogamodeme,* this is a relatively isolated, naturally interbreeding, population (gamodeme) occupying a particular area (LINCOLN *et al.*, 1982).

5. COMMENTS AND DISCUSSION

Although I have no simple solution to offer, it might be worth discussing the mechanism(s) that could explain the partial genetic isolation of the close neighbouring Hansa Bay *Oliva* populations. Interpopulation gene flow depends upon dispersal and this could take place either at the larval or at the adult stage.

Nothing is known about the vagility of *Oliva* larvae, but the present observations

suggest that it must generally be low. Indeed, the larval stage lasts several days (OLSSON & CROVO, 1968; TURSCH, 1991) and the seasonally variable currents could easily transport pelagic veligers anywhere in Hansa Bay within hours. It has been shown that the veliger of *Olivella verrauxii* is not pelagic but swims on the bottom (MARCUS & MARCUS, 1959). I could find no report of *Oliva* larvae being caught in plankton hauls. Even if the larvae were effectively dispersed, successful immigration could still be severely restricted by the necessity of settling on a suitable substrate. Effective larval dispersal over large distances certainly does take place, as evidenced by the very large distribution of several *Oliva* species, but it must be quite infrequent.

The *Oliva* populations of Hansa Bay are so closely spaced that immigration could possibly also occur at the adult stage. Very little is known about the actual cruising range of adult *Oliva* species. They can live several years and do easily reach speeds of 25 cm/min (TURSCH, 1991). Tracks several meters long are frequently observed and an *Oliva* could conceivably travel many kilometers in its lifetime. One could even imagine that adult *Oliva* could cross small stretches of moderate depths: they have no pressure-sensitive organ and they could certainly tolerate reduced light (being mainly nocturnal, see VAN OSSELAER & TURSCH, 1993). In addition, they can easily subsist on a wide variety of foods that are completely foreign to them.

In theory, *O. oliva* could thus travel from Boro to the black Sisimangum beach in a matter of days or weeks. But no specimen of the "Boro type" has ever been collected from Kalagima to Awar. Conversely, no specimen of the "Sisimangum type" has ever been caught at Boro Beach. It is doubtful that the mouth of the Sakula river could constitute a serious barrier: it is only about 10-20 m wide and is completely closed by a sand bar at low tide during the dry season. The similar (but smaller) Awar river does not divide the Sisimangum population. It is more likely that the obstacle is constituted by the small rocky point separating Boro from Kalagima, where the soft substrate that all olives require is found at 5-6 m, an environment possibly unsuitable for a species restricted to surf beaches. This same rocky point is no obstacle for *O. smithi* that often lives in deeper water. In practice, adult Olives seem rather sedentary, as shown by the lagoon population of *O. smithi* (see section 3.2, §2). One could conjecture they are prevented from moving by being very sensitive to minute changes in the nature of the substrate, but this is unlikely because in sediment choice experiments, several species of *Oliva* have shown only very slight substrate preferences (VAN OSSELAER & TURSCH, 1993). One could also imagine that the micropopulations are kept together by some cohesive force such as chemical attractants (TURSCH, 1991) but no firm data yet support this hypothesis.

6. CONCLUSIONS

The *Oliva* species of Hansa Bay consist in a mosaic of populations, the map of which fairly reflects the discontinuities of the habitat. These populations are not only ecological races; in many cases they also appear to be temporarily isolated by restricted gene flow, even over very short distances. Neighbouring, conspecific populations frequently differ to the point of complete morphological separation. That different populations could be distinguished by some combination of characters is no great discovery and was indeed fully expected (see MAYR, 1969 and FUTUYMA, 1986), even for shells that are collector's favourites. The observations at Hansa Bay just give a somewhat sharper image of the spatial scale, the extent and the tempo of intraspecific variation in the genus *Oliva*. They also point to the necessity of moderating the current taxonomic approach to this genus.

First, the scale of sympatry in *Oliva* can be much smaller than it is generally considered. The pattern observed in tiny Hansa Bay is certainly not unique and can be expected to occur over the very large distribution areas of many species. In addition to the examples given in the introduction (see TURSCH *et al.*, 1992), the populations of *Oliva oliva* I have sampled in two very similar small bays separated by only 5.8 km on the North coast of Hon Lon Island, off Nha Trang (Vietnam) can be separated at a glance. Many other similar examples could be given and it is a safe bet that morphological discontinuities between close-set populations will be commonly observed in any careful field study of *Oliva*.

Special caution is thus necessary in the application of our most reliable tool for taxonomic decisions at the morphospecies level: the demonstration of morphological gaps between sympatric populations (see Introduction). When comparing populations from a same, broad locality, data such as "New Guinea, shallow

water" or even "Hansa Bay, sand, 8 m" are now clearly insufficient to demonstrate sympatry.

We can be sure that *Oliva* populations are sympatric only when they actually overlap in space. This can be known only if specimens of both taxa have been observed together (or within a short distance) in the same, continuous microhabitat. Such a relationship could be described by the word "*syntopic*" in a slightly restricted sense. "Syntopic" has been defined as: "pertaining to populations or species that occupy the same macrohabitat, *are observable in close proximity* (italics are mine) and could thus interbreed" (LINCOLN *et al.*, 1982). Conversely, in the absence of actual spatial overlap, one could use the word "allotopic" in the somewhat restricted sense of "*not observed in close proximity*".

In the case of *Oliva* (at least) it is obviously safer to replace our broad criterion of sympatry by that of syntopy. This does not upset any fundamental concept, as it is only a reduction of spatial scale. It will actually facilitate the task of the taxonomist because differences between similar species will generally be more pronounced wherever these species come into contact (the well-known phenomenon *of character displacement*).

Without this reduction of the commonly accepted scale of sympatry, one could be led to create as many *Oliva* "species" as there are local populations within an arbitrary range of proximity. Many "species" of *Oliva* have indeed been created upon differences smaller than those observed between some of the Hansa Bay conspecific populations. This solution is unfortunately attractive to some (see the criticism of MAYR, 1969) but is demonstrably wrong. In all the cases studied so far in this laboratory and for which enough data were available (for example the protean "*Oliva oliva* complex", see TURSCH *et al.*, 1992), the set of all conspecific populations (considered over the whole distribution range) always form a morphological continuum. The characters discriminating any two given conspecific populations are invariably bridged by at least another population (or by a chain of intergrading populations). This indicates that gene flow, even if restricted, does nevertheless take place.

Some could then be tempted to consider each of the morphologically distinct local populations of *Oliva* as a subspecies in the sense of "local variety". This would lead to obvious nomenclatural excess and the notion of subspecies (largely a category of convenience) would then lose any meaning. The sensible definition of MAYR (1963) restricts subspecies to "aggregates of populations", on much larger spatial scale.

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Noradrenaline and adrenaline in the cerebral ganglia of the giant African land snail *Achatina fulica* Bowdich.

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KEYWORDS : *Achatina fulica*, cerebral ganglia, noradrenaline, adrenaline.

ABSTRACT. Both histochemical and biochemical studies were conducted to note the state of noradrenaline and adrenaline in the cerebral ganglia of the giant African land snail *Achatina fulica* Bowdich. The occurrence and distribution of noradrenaline and adrenaline containing granules in the cerebral ganglia have been noted following histochemical studies. It is revealed that the noradrenaline and adrenaline containing granules are distributed to central and peripheral regions of the ganglia respectively. The amount of fluorometrically estimated noradrenaline in the cerebral ganglionic tissues was almost equal to the estimated amount of adrenaline.

INTRODUCTION.

The occurrence and distribution of monoamines in the cerebral ganglia of molluscs have been the subject of study by many workers. Thus, catecholamine containing cell bodies have been demonstrated in *Limax maximus* Linnaeus (OSBRONE and COTTRELL, 1971), *Aplysia* (GOLDSTEIN, 1984), *Helisoma* (TRIMBLE et al., 1984), *Helicella virgata* Da Costa (FRANCHINI et al., 1985) and *Lymnaea stagnalis* Linnaeus (AUDESIRK, 1985). The distribution of monoamines in the central nervous system of the gastropods, *Hermissenda crassicornis* Eschscholtz and *Achatina fulica* Bowdich has also been described by CROLL (1987a, b, 1988). VON EULER (1953) reported the presence of noradrenaline in *Octopus*. MCCAMAN et al. (1979, 1984) were successful in isolating dopamine, 5-Hydroxytryptamine and N-acetyldopamine from molluscan ganglia. HERNADI et al. (1989) demonstrated the distribution of serotonin (5-HT)-containing neurones in the central nervous system of the land snail *Helix pomatia* Linnaeus. Distribution of dopamine in the central nervous system of the pond snail *L. stagnalis* has also been studied by ELEKES et al. (1991) and WERKMAN et al. (1991). Even, studies on chemical transmission in invertebrate central nervous system have been made by GERSCHENFELD (1973). The present study provides qualitative and quantitative accounts of noradrenaline and adrenaline in the cerebral ganglia of the giant African land snail, *A. fulica*.

MATERIALS AND METHODS.

Adult *Achatina fulica* Bowdich were collected from local vegetable gardens in October, 1987. They were 68.0-71.0 mm in shell length, 32.0-34.5 mm in shell breadth and 36.74-40.65 g in body weight. The snails were anaesthetized by applying chloroform and the cerebral ganglia were quickly dissected out for both the histochemical and biochemical determinations of noradrenaline and adrenaline. The snails were anaesthetized under field conditions and the samples were collected immediately after the same. The following methods were used in the study.

Histochemical method.

Control.

Cerebral ganglia dissected out from five *A. fulica* were immersed in Carnoy's fixative, embedded in mixture of Beeswax, cerecin and paraffin and 30 µM sections were cut.

Chromate-dichromate reaction.

For total catecholamines, cerebral ganglia dessected out from five *A. fulica* were treated with a mixture of 5% potassium dichromate and 5% potassium chromate (10:1) solutions for 48 hours and subsequently transferred to 10 % formalin for 24 hours (HILLARP and HÖKFELT, 1955). Then, the cerebral ganglia were

embedded in a mixture of Beeswax, ceresin and paraffin for a period of 30 minutes and required 30 μM sections were prepared.

Iodate reaction.

To detect noradrenaline, cerebral ganglia dessected out form five *A. fulica* were fixed in saturated solution of potassium iodate for 24 hours and in turn these were immersed in 10 % formalin for 48 hours (HILLARP and HÖKFELT, 1955). After a 30 minute embedding in a mixture of Beeswax, ceresin and paraffin 30 μ M sections were prepared.

Biochemical method.

Cerebral ganglia of twelve other snails (*A. fulica*) were processed for spectrophotofluorometric determinations of noradrenaline and adrenaline. Noradrenaline and adrenaline were extracted and purified following the method of COX and PERHACH (1973) and estimated according to the method of LAVERTY and TAYLOR (1968). The cerebral ganglia of four snails were sorted for each measurement. Three such samples were considered for reading by a Hitachi (Model 650-10 M) fluorescence spectrophotometer (for details see MAHATA and GHOSH, 1989). The mean of three readings was taken as the final data. Student's 't' test (SNEDECOR and COCHRAN, 1967) was applied for statistical analysis of the data.

RESULTS.

Histochemistry.

Control.

No colouration was observed either in the central or peripheral region in the cerebral ganglia of *A. fulica* Bowdich (Figure 1).

Treatment.

Following treatment with potassium chromate-dichromate solution, numerous brown and yellow coloured granules were noted in cerebral ganglionic tissues of the snail, *A. fulica*. The yellow coloured granules (indication of presence of noradrenaline) were exclusively confined to central portion of the cerebral ganglia (Figures 2, 4) while the brown coloured granules (indication of presence of adrenaline) were distributed to the peripheral region of the cerebral ganglia (Figures 3,5).

The occurrence of yellow granules (indication of presence of noradrenaline), in an irregular fashion in the central portion of the tissues was also noted following potassium iodate treatment (Figure 6).

Biochemistry.

The spectrophotofluorometric determinations revealed that the cerebral ganglia of *A. fulica* contain both noradrenaline 14.09 ± S.E. 0.80 μg/g tissue weight) and adrenaline (12.24 ± S.E. 0.61μg/g tissue weight). However, such difference in amount is not statistically significant ($t_{c/2}$; 4 = 2.776, P = 0.05).

DISCUSSION.

HILLARP and HÖKFELT (1955) were successful in establishing the presence of noradrenaline and adrenaline in vertebrates. The results of the present studies clearly demonstrate that this technique is equally effective in determining the noradrenaline and adrenaline in invertebrates also. It is clear that both noradrenaline and adrenaline are present in the cerebral ganglia of *A. fulica*. The brown granules are seen following reaction with potassium chromate-dichromate solution, indicate the occurrence of adrenaline in the cerebral ganglia, and the yellow granules probably represent the presence of noradrenaline. The appearance of yellow coloured granules following potassium iodate treatment further confirms the existence of noradrenaline in the cerebral ganglia.

Using histochemical fluorescence technique CROLL (1987 b, 1988) noted the distribution pattern of catecholaminergic neurons in the central nervous system of juvenile *A. fulica*. The results of the present histochemical studies indicate that the monoamines noradrenaline and adrenaline are confined to the central and peripheral regions of the cerebral ganglia respectively.

Since the snail specimens considered for studies were procured from similar conditions and the amount of noradrenaline and adrenaline recorded is almost same in quantity, it may be said that under static physiological conditions of an animal, these two amines would be released in equal quantity.

An independent and concurrent study of catecholamines in the nervous system of several gastropod and bivalve molluscs demonstrated the presence of 5-Hydroxytryptamine and dopamine, in relative abundance, in these forms (DHAL et al., 1962; SWEENEY, 1963 ; LEAKE and WALKER, 1980). Though HILL and WELSH (1966) were doubtful OSBORNE and COTTRELL (1970) and JURIO and KILLICK (1972) were very much sure about the presence of noradrenaline and adrenaline in molluscs. The quantitative estimation of these amines occurring in the

central nervous system of *H. aspersa* ruled out any kind of confusion (OSBORNE, 1984). Measurement of noradrenaline and dopamine in larval and spat stages of the Pacific Oyster *Crassostrea gigas* (Thunberg) by COON and BONAR (1986) and quantitative fluctuations of noradrenaline and adrenaline in the garden slug *Laevicaulis alte* (Férussac) (PANIGRAHI et al., 1992, 1994) strengthen the confidence further more. The results of the present studies providing not only additional confidence regarding the occurrence of noradrenaline and adrenaline in *A. fulica* but also supplying information on the distribution of these amines in the central nervous system.

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Figures 1-6 (opposite page).

Figure 1. Section of cerebral ganglia of *Achatina fulica* fixed with Carnoy's fixative (Control). [Central and peripheral regions of the section are free from any noticeable change]. (X165)

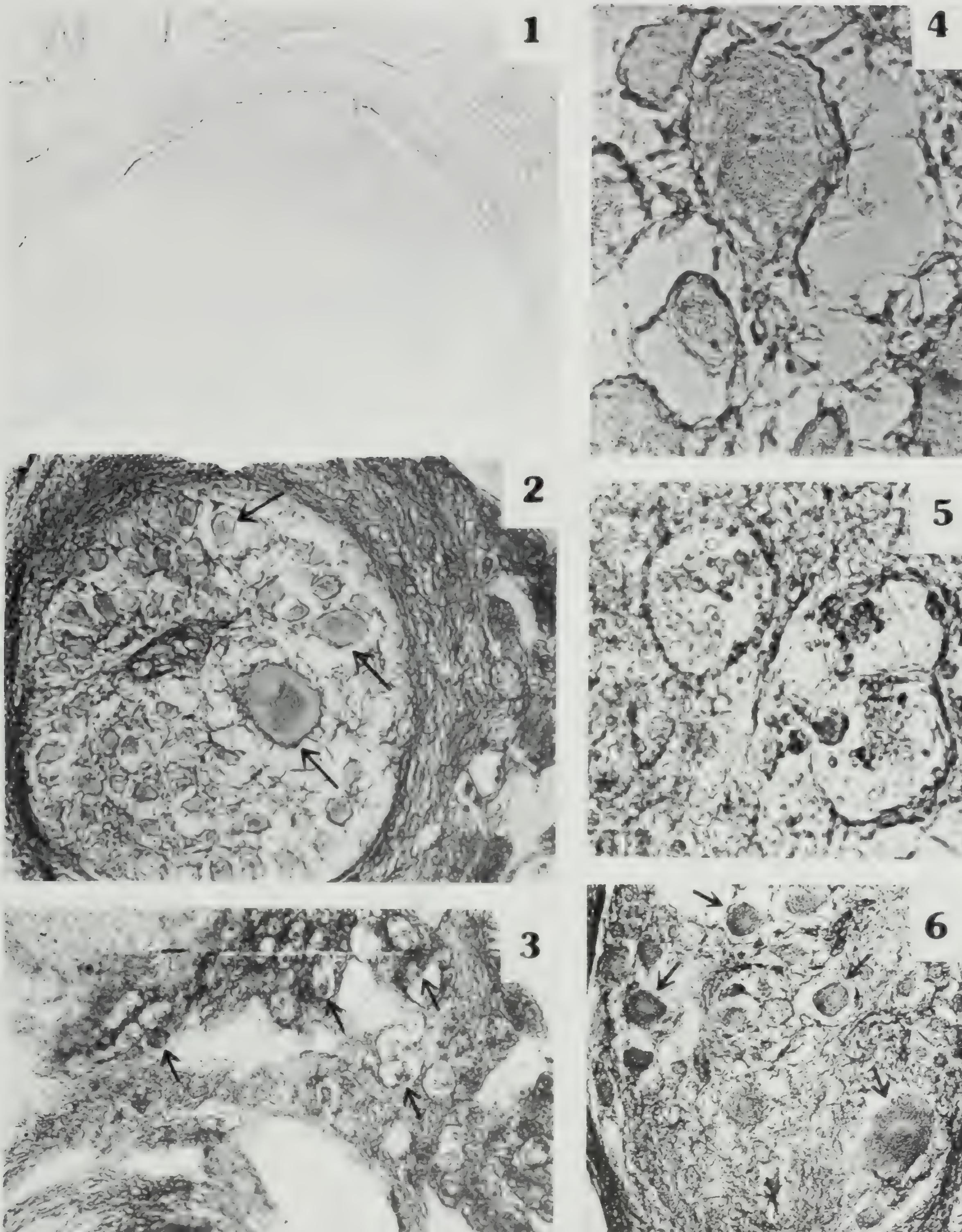
Figure 2. Noradrenaline (some are indicated by black arrows) and adrenaline (some are indicated by white arrows) containing granules following treatment with potassium chromate-dichromate solution in the cerebral ganglia of *Achatina fulica*. (X140)

Figure 3. Adrenaline containing granules (some are indicated by arrows) following treatment with potassium chromate-dichromate solution at the peripheral region in the cerebral ganglia of *Achatina fulica*. (X160)

Figure 4. Photomicrograph showing noradrenaline containing granules occurring in the central region of cerebral ganglia of *Achatina fulica* [enlarged view of the central part of Figure 2]. (X580)

Figure 5. Photomicrograph showing adrenaline containing granules occurring in the peripheral region of cerebral ganglia of *Achatina fulica* [enlarged view of Figure 3]. (X510)

Figure 6. Distribution of noradrenaline containing granules (few are indicated by arrows) in the central part of cerebral ganglia of *Achatina fulica* following treatment with potassium iodate. (X140).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